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STRUCTURAL AND TOPOCHEMICAL CHANGES
IN THE EGG CELLS OF
LIMNAEA STAGNALIS L. DURING OOGENESIS

by

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The structural and topochemical relations of the freshly-laid egg of *Limnaea*, as described by RAVEN (1945), arise gradually during oogenesis from the much simpler structure of the early oocyte. In order to obtain a better understanding of the structure of the full-grown egg cell, which formed the object of our experimental researches (RAVEN and BRETSCHNEIDER 1942 and further papers, cf. RAVEN 1948), an extensive investigation of oogenesis seemed desirable. This investigation had to include the study of various cell compounds by cytochemical methods. In this way, it should be possible to get some insight into the presumable interrelations of these diverse compounds in a cell with a high and very active metabolism. Besides a qualitative study of the origin of the structural and chemical differentiations of the egg also their relations with the growth of the egg cell should be studied quantitatively.

In order to get comparable results, the same cytochemical reactions have been employed as in our former papers (RAVEN and BRETSCHNEIDER 1942, RAVEN 1945, 1946). The quantitative determinations of cell compounds have been made by means of centrifuge experiments. The snails were centrifuged in toto for 10–15 minutes at a centrifugal pressure of $1860 \times$ gravity; immediately afterwards, the gonads were excised and fixed. From the sections, the layers of cell substances stratified by centrifugation were drawn on cardboard at a constant magnification, and the drawings were cut out and weighed. In this way, the relative volumes of the cell compounds were determined; by comparison with the actual total volume of the egg cell they can be reduced to actual volumes (in μ^3). In most of the diagrams, however, for the sake

of simplicity not the actual cell volume, but the product of length and breadth of the largest section of the cell (called "cell-index") has been used as a measure of cell size. Since the measurements have all been made on fixed and sectioned material, the values found are less than those observed by RAVEN (1945) on living eggs, in consequence of shrinking during dehydration and embedding of the gonads.

THE ANALYSIS OF OOGENESIS

I. PHASES AND RATE OF DEVELOPMENT

During oogenesis various phases of multiplication, growth, differentiation and rest may be distinguished. From the study of young *Limnaea*'s reared from the eggs the duration of these phases, at least as regards the first generation of eggs, could be determined. The characteristics, sequence and duration of these phases have been summarized in fig. 1.

a. From primary sex cell till oogonium

The first phase of development, beginning with the fertilized egg (A) and ending with the oogonia (D) of the recently-hatched young snail, is characterized by a period of intensive division of the egg cell, during which the primary sex cells are formed. This phase lasts 30 days; 15 days are taken up by embryonic development till the formation of the gonadal anlage, whereas the postembryonic development of the latter with the multiplication of the primary sex cells (C) and their transformation into oogonia takes another 15 days.

b. Amoeboid phase

In the hermaphroditic gonad the egg cells develop, as contrasted with the spermia, between the connective tissue and the epithelium lining the cavity of the ovariotesis. In this retroepithelial position, the egg cells show an intense amoeboid motility (E). They swarm out from a germinal centre to various positions in the acini of the gonad. This phase, which lasts 6 days, is characterized by an initial growth of the early oocytes (cell index increasing from 170 to 1200 μ^2). Their shape is very variable, and true pseudopodia are present.

c. Growth phase

Now the oocyte becomes sessile and is surrounded with nutritive cells apically and laterally, which form a follicle around the egg; only its basal part borders upon the connective tissue (F). Most of the phenomena of growth and differentiation described below occur during this

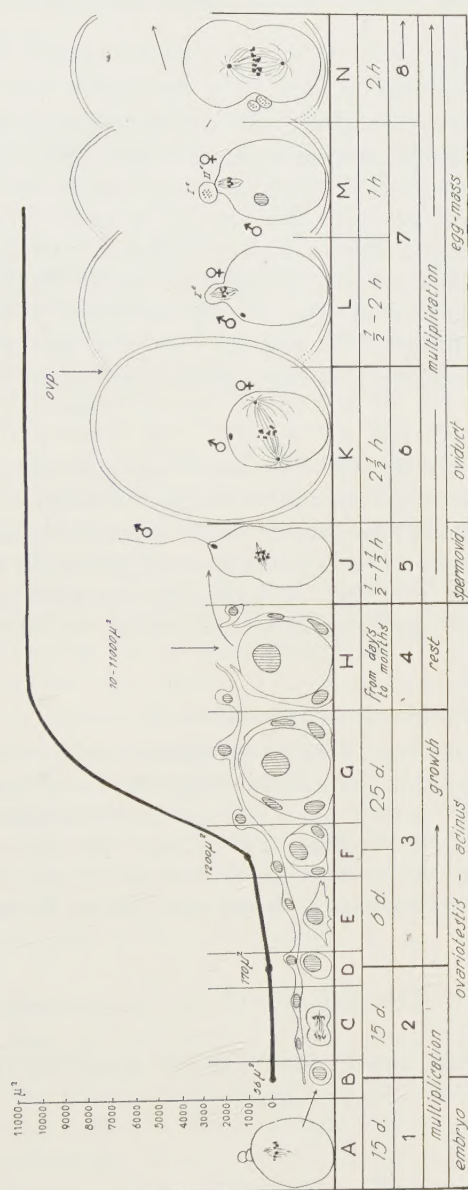


Fig. 1. Diagram of phases of life cycle of *Limnaea* egg. A. Embryonic development, B. Formation, C. Multiplication of primary sex cells, D. Oogonia, E. Amoeboid phase, F. Formation of follicle, G. Growth phase, H. Rest phase, I. Insemination phase, K. Phase of prae-maturity, L. First maturation division, M. Second maturation division, N. First cleavage, beginning of embryonic development. Ordinates: cell-index

N. First cleavage, beginning of embryonic development. Ordinates: cell-index

phase (F-G). It lasts, at least as regards the first generation of eggs, about 25 days, during which the cell index increases from 1200 to 11000 μ^2 .

d. Rest phase

When the oocyte has reached this size and the corresponding degree of differentiation, a rest phase begins, during which no changes of importance are to be noted (H). With the first generation of eggs in the young snail about 40 days go by until the first oviposition takes place. In the full-grown *Limnaea* this rest phase will vary, according to the season, from a few days between subsequent ovipositions in summer to a period of many months in winter. Finally, ovulation takes place; by autolysis both of the follicle cells and the overlying acinus epithelium the full-grown oocyte passes into the lumen of the gonad.

e. Insemination phase

After ovulation the course of development is accelerated a great deal; the subsequent phases follow each other within the scope of hours. The ovulated oocytes enter into the sperмовидuct, where they assemble and insemination takes place (I) (BRETSCHNEIDER 1948a). As a rule, they stay in the sperмовидuct for $\frac{1}{2}$ -1 $\frac{1}{2}$ hour only, but when a stagnation in the formation of the egg-mass occurs this period can increase to one day (in summer).

f. Phase of prae-maturity and egg-mass formation

After insemination the egg cells pass the various parts of the oviduct, where they are surrounded with perivitelline fluid and capsule membrane and cemented together by a viscous mucus substance into an egg-mass (BRETSCHNEIDER 1948b). The passage through the oviduct lasts about 2 $\frac{1}{2}$ hours. Meanwhile, in the oocyte the preparatory processes of the subsequent meiotic divisions take place (RAVEN 1945).

g. Meiotic phase

Oviposition is followed immediately by the first maturation division, which is finished $\frac{1}{2}$ -2 hours after oviposition (L) and is followed shortly afterwards by the second maturation division, which takes place 1 hour after the first (M) (RAVEN 1945).

h. First cleavage

With first cleavage, which occurs 2-3 hours after the second maturation division, embryogenesis begins, which leads, at average room temperature in summer, to the formation of a young snail ready to hatch in 15 days.

2. GROWTH OF THE CYTOPLASM

The early mobile oocyte consists chiefly of cytoplasm and nucleus. The cytoplasm has a very dense structure and stains heavily with all basic stains. After the egg has settled in the follicle and the yolk begins to appear in its centre, a broad zone of hyaline plasm at the periphery remains free of inclusions. During the growth phase hyaloplasm is accumulated especially at the apex of the cell. Part of this sinks into the depth unto the nucleus, which it surrounds as a perinuclear plasm. In the full-grown oocyte only a thin layer at the periphery (cortical plasm) keeps its hyaline appearance; the remaining cytoplasm is interspersed between the numerous inclusions as ground plasm. The basophily of the cytoplasm diminishes during growth. The cortical plasm has a finely vacuolar appearance after most of the fixatives employed. Peripherally it is bounded by the oolemma, towards the endoplasm by a layer of fine granules. Often the vacuoles show a radial arrangement, which gives a radially striped appearance to the cortical plasm. Whereas most of the hyaline plasm is accumulated in a transparent middle zone in centrifuged eggs, a rather considerable part of it remains in between the yolk granules in the centrifugal yolk zone; this part cannot be determined quantitatively. Therefore, the following determinations are restricted to the size of the hyaline layer. The cytoplasm volume of the earliest oocyte amounts to $1\ 112\ \mu^3$ (63 % of the total cell volume), that of the full-grown oocyte to $249\ 320\ \mu^3$ (40 % of the total volume). Hence, the cytoplasm increases during growth to 223 times its original volume. Part of this increase may be due to hydration. The cytoplasm has no fixed structure, but shows a certain mobility of its parts as revealed by phenomena of cytoplasmic flow; already 4 hours after centrifuging the living snail, stratification of the egg cells has disappeared again and the egg inclusions are redistributed. The eggs of these snails develop entirely normally.

3. NUCLEAR GROWTH AND NUCLEOPLASMIC RATIO

In oogenesis vegetative and generative phenomena occur successively. The production of paraplastic cell inclusions, accompanying growth, precedes the formation of chromosomes and the phenomena of maturation and fertilization. During growth of the egg all visible changes of the generative parts of the nucleus stop; the chromosomes become invisible and the vegetative function of the nucleus prevails. The synthetic activity of the nucleus can be deduced from the parallel growth of nucleus and cytoplasm and the interactions between both which are partly visible. The nucleus of the earliest mobile oocyte has a size of

$650 \mu^3$ (37% of total cell volume), that of the full-grown oocyte measures $105\,000 \mu^3$ (17%). Hence, the nucleus increases during growth to 162 times its initial volume. The nucleoplasmic ratio decreases in this period from 1:1.7 to 1:2.4. When this ratio is computed, however, in relation to the total egg with all its paraplasmic inclusions, its decrease is greater; moreover, when the average ratio is recorded against time, a S-shaped curve is obtained (fig. 2). Initially, growth of

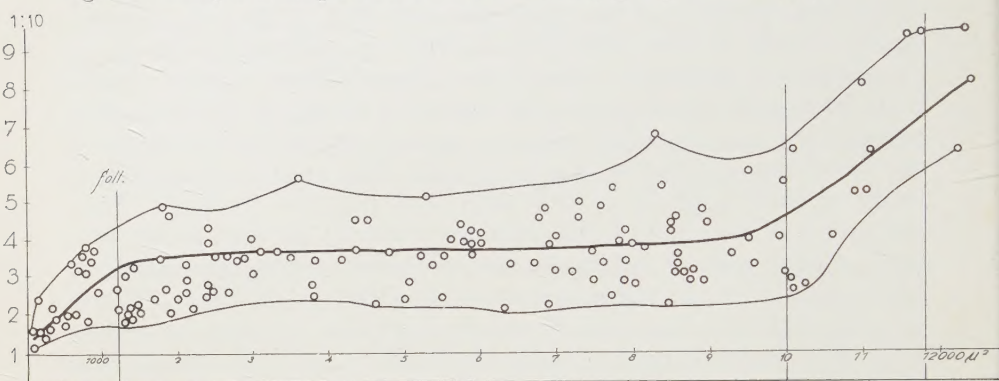


Fig. 2. Diagram of nucleoplasmic ratio (nuclear volume against total cell volume). Abscissae: cell-index. Ordinates: inverse of nucleoplasmic ratio. Each circle represents a single determination

the cell is greater than that of the nucleus, then a long period of nearly synchronic growth follows, finally, during the rest phase a diminution of the nucleus occurs, followed by its dissolution. The single values are widely scattered, however, about the average curve. This cannot be accounted for entirely by random variation or errors of measurement. The principal cause of these variations in nucleoplasmic ratio has to be sought in a periodic shrinking and swelling of the nucleus, whereas the cell, presumably, shows a regular growth. The nucleus during growth repeatedly deviates from its spherical shape and shows local foldings by unilateral contractions of the nuclear membrane (fig. 5). From the high frequency of these deformations and from other morphological indications it is evident that during the growth phase alternately high and low surface tensions of the nucleus occur, which give rise to a rhythmical pulsation of the latter.

4. THE NUCLEOLUS

The remarkably extensive form changes and signs of activity of the nucleolus during oogenesis induced us to a further analysis of this structure. The nucleus of the earliest oocyte possesses two nucleoli of unequal

size which derive from the oogonium: the bigger eunucleolus with a diameter of 4μ and a smaller paranucleolus of 2μ . The changes to be described concern only the persisting eunucleolus; the paranucleolus disappears, as a rule, already in the earliest oocyte stage. The size of the eunucleolus increases continuously till the middle of the growth phase of the oocyte, from 4μ to 20μ in diameter; then its size decreases again (fig. 3). Just as with the nucleus as a whole, the single values of nucleolar

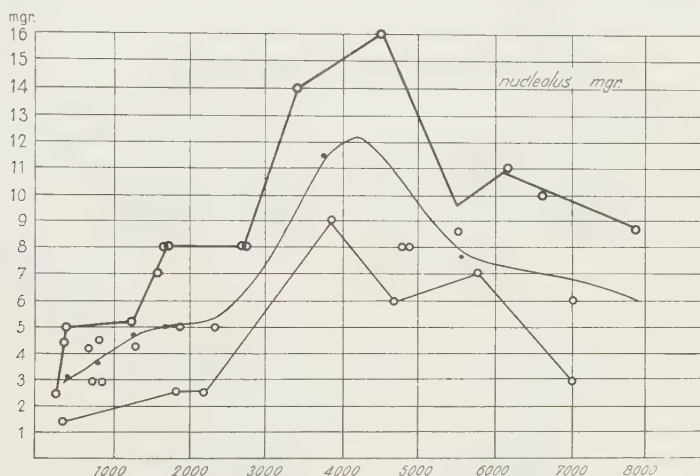


Fig. 3. Diagram of volume of eunucleolus during growth phase. Abscissae: cell-index. Ordinates: volume of eunucleolus (in arbitrary units)

size are widely scattered about the average curve; it appears that this is due to variations in the size of the nucleolus by production and extrusion of substances. The secretory activity of the nucleolus is apparent from the changes in appearance it undergoes during development. The primordium of the nucleolus in the earliest oocyte is uniformly acidophil, whereas at the end of oocyte development the nucleolus shows a homogeneous basophil appearance (fig. 4). In between diverse appearances occur, indicating an intense activity. This diversity may be reduced to a few principles.

The nucleolus consists of an endonucleolar plasm, which is originally homogeneous, and a cortical layer surrounding it. It often shows a pronounced heterochromatic staining, the cortical layer staining differently from the endonucleolar plasm (so-called amphinucleolus). Thereby both parts may be alternately acidophil or basophil; evidently, these are no constant properties, but temporary conditions which may pass over into each other quite easily.

The formation of nucleolar products obviously can take place in two

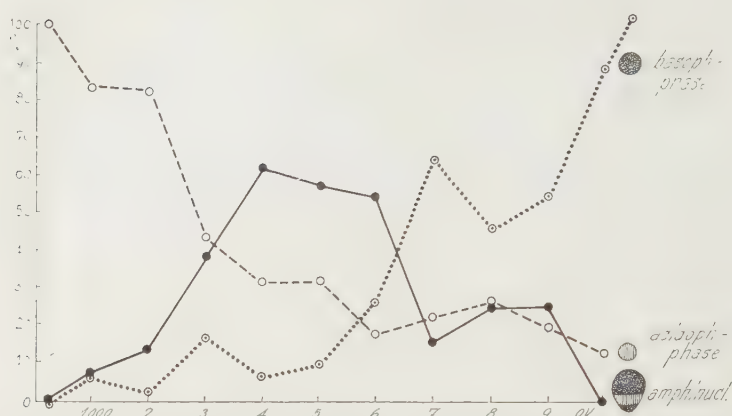


Fig. 4. Percentage of acidophil, basophil and amphinucleoli during growth phase
Abscissae: cell-index

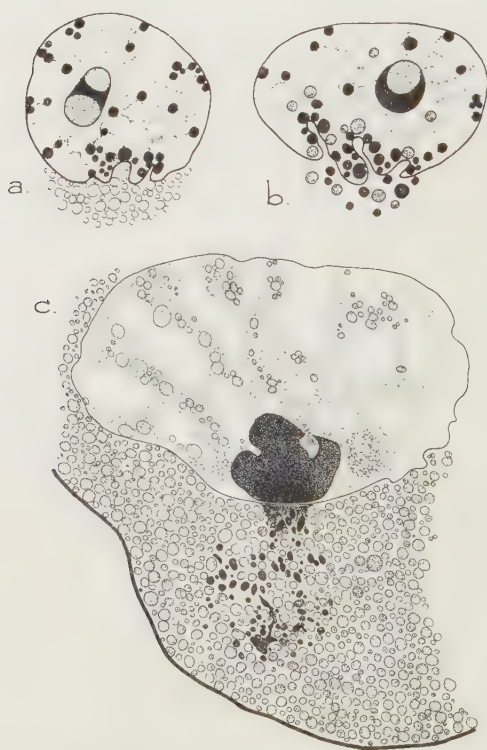


Fig. 5. Extrusion of formed substances through the nuclear membrane into the cytoplasm

ways. Firstly, an intranucleolar production occurs by the formation of vacuoles in the homogeneous endonucleolus, which increase in size or number with simultaneous decrease of the endonucleolar ground substance. The observations seem to prove that the formed product in the vacuoles may be fluid or granular or have a highly viscous consistency. It may flow into the karyolymph through a visible pore or by breaking through the cortical layer of the nucleolus. Sticky colloidal substances

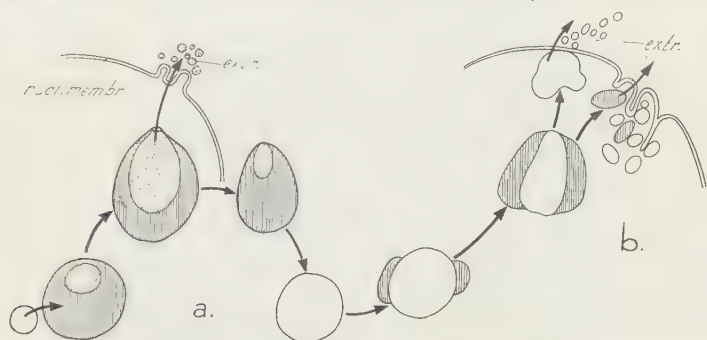


Fig. 6. Intranucleolar (a) and epinucleolar (b) product formation in the growing oocytes of *Limnaea*

are pinched off in form of drops. Apparently, the much reduced remainder of the nucleolus may grow again and resume its activity. The intranucleolar product formation may take place at two opposite points, whereby dumbbell-shaped nucleoli are formed.

The second type of product formation is an epinucleolar one, whereby the product originates in the cortex, which thickens locally and grows out into a granulum; this is pinched off subsequently. The formed product differs from the nucleolar substance in its staining capacity. Product formation may occur unilaterally or bilaterally; in the latter case, as a rule the whole nucleolus breaks down into several pieces. Often the extrusion of formed substances through the nuclear membrane into the cytoplasm may be observed (fig. 5); this is especially clear in those cases where they show a basophil staining. Smaller nucleolar granules collect between the folds of the nuclear membrane; probably, they pass the membrane in form of a viscous fluid. Similar appearances have been observed already by LUDFORD (1922) in the nucleolus of egg-cells of *Limnaea* and *Patella*.

The various appearances of the nucleolus are met with during oocyte development in regular succession. Homogeneously acidophil nucleoli, originally the only type, decrease from 100 % at the outset to 12 % at the end. The uniformly basophil type, which is lacking in the beginning, increases towards the end to nearly 100 %; with the commencement of

maturation these basophil nucleoli are resorbed. Probably, the intranucleolar secretion is a polyphasic one; after extrusion of the product restitution occurs. On the contrary, the bilateral epinucleolar product formation is irreversible and monophasic; this type is only met with towards the end of oogenesis (fig. 6).

In centrifuged oocytes the nucleolus is displaced centrifugally; in most cases, it causes a hernia of the nucleus to appear in consequence

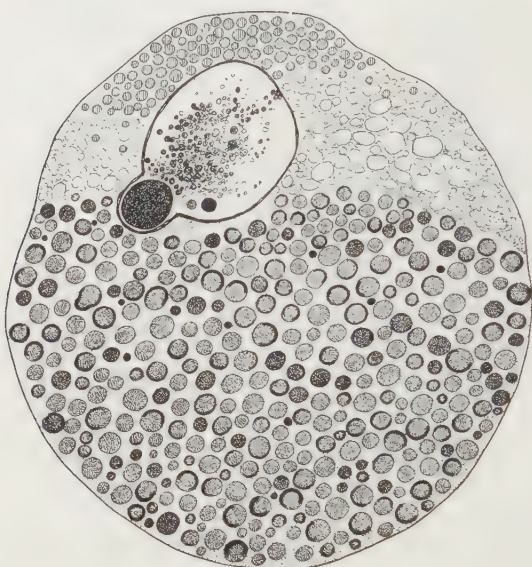


Fig. 7. Centrifuged oocyte of *Limnaea*; nucleolus in hernia of nuclear membrane

of its high specific gravity (fig. 7). This hernia may be pinched off with longer centrifuging, whereby the nucleolus gets into the yolk zone. The amphinucleolus stratifies into a heavier and a lighter compound; often vacuoles are flung out of the nucleolus.

5. GENESIS OF THE PROTEID YOLK

Among the paraplasmic reserve substances of the full-grown oocyte the proteid yolk, occupying nearly 50% of the total cell volume, takes a predominant place. It consists of granules of uniform size, called β -granules by us (RAVEN and BRETSCHNEIDER 1942); they show the usual protein reactions. In the normal egg they show a regular distribution; after centrifuging, they are accumulated centrifugally (fig. 7, 8). The earliest mobile oocyte does not yet contain any proteid yolk. The first



Fig. 8. Centrifuged oocyte. Stratification into fat zone, hyaloplasm with germinal vesicle and yolk zone

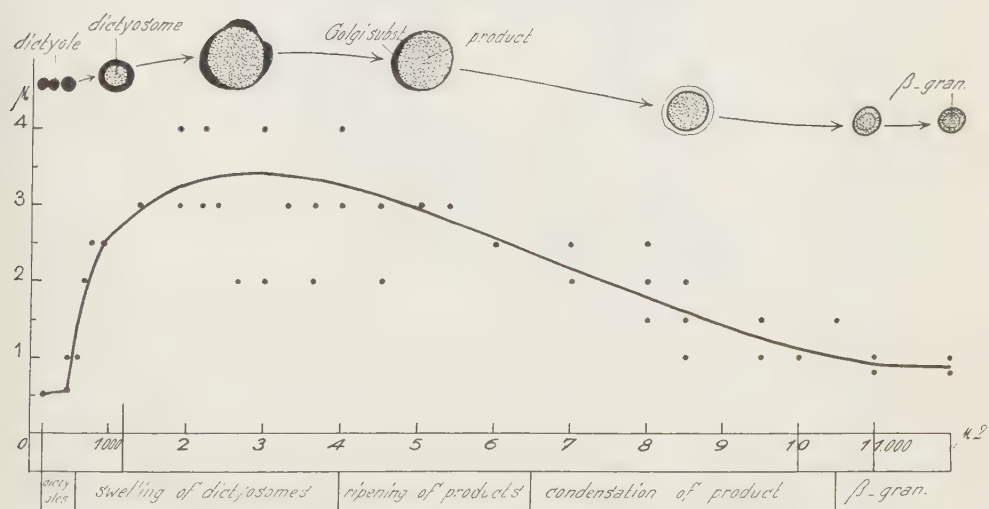


Fig. 9. Formation of β -granules by the activity of Golgi bodies. The graph shows the accompanying changes in size of granules. Abscissae: cell-index. Ordinates: diameter of granules

yolk granules appear in an oocyte of $1760\mu^3$ in the Golgi field ("Balbiani's nucleus"); from this moment on, a gradual increase takes place. From measurements of the biggest granules in each phase of development it becomes clear that every granule passes through a definite developmental cycle. It begins as a small spherule with a diameter of 1μ , then grows to a diameter of $3-4\mu$; afterwards, it diminishes in size, presumably by condensation and loss of water, to possess a diameter of 1.5μ at the end of the growth phase. Hence, during the first half of the growth phase the average size of the proteid granules is greater than in the second half (fig. 9).

6. GAMMA-GRANULES

Besides the above-mentioned proteid yolk still another kind of protein granules is found in the oocytes, the so-called γ -granules (RAVEN and BRETSCHNEIDER 1942). Their number is much less than that of the β -granules; they are mostly oblong and have a diameter above 4μ . Apparently, they differ in chemical composition from the β -granules and, for a long time, their specific gravity is less. They can be dis-

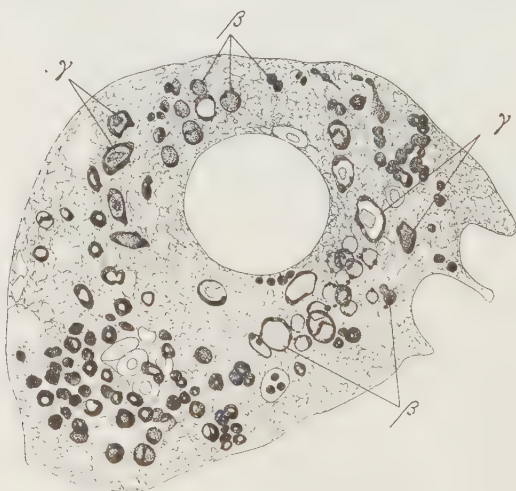


Fig. 10. Formation of β - and γ -granules in growing oocyte of *Limnaea*

tinguished already during their formation by their oblong shape (fig. 10). After they have reached their definite size, they show a pronounced acidophily, especially after alcohol fixation. During the passage of the full-grown egg through the oviduct the first indication may be seen of the peculiar swelling, which characterizes them at later stages (RAVEN

1945). Since their specific gravity varies very much (in the freshly-laid egg they are still heavier than the β -granules, after swelling they belong to the lightest components of the egg, RAVEN 1945), they form no definite layer in centrifuged eggs; therefore, a quantitative determination of their volume is not possible.

7. GOLGI SUBSTANCE

The Golgi substance has been studied according to NASSANOV's method with osmic acid, after POLL with formol-osmium and according to DA FANO with silver nitrate. The impregnated sections have been compared with azan-stained preparations.

In the earliest mobile oocyte the Golgi field which has a diameter of about 5μ is found next to the nucleus; it is derived from that of the oogonium. It consists of a basophil ground plasm with a few granules, which possess an osmio- and argentophil surface layer. Already with the beginning of the amoeboid phase of the oocyte this Golgi field disperses into single granules, among which two kinds may be distinguished: granules of about $0,6\mu$, which are wholly impregnated, the dictyoles; and bigger granules, the dictyosomes, which have a clear centre consisting of protein (the Golgi internum) and an osmiophilic periphery. Both granules multiply by division (dictyokinesis), whereby more and more elements are produced, which disperse in the cytoplasm. In the dictyoles a clear osmiophobic centre appears forming the first germ of the future proteid granule and, according as it grows, the peri-

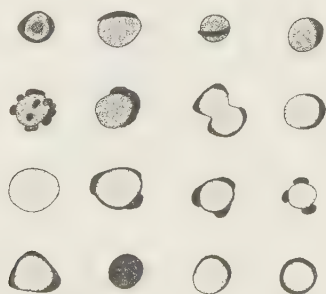


Fig. 11. Various appearances of the dictyosomes after osmium impregnation

pheral osmiophily decreases; finally, the Golgi substance no more completely surrounds the granule, but forms a terminal cap or band (fig. 11). As soon as the granule has reached a size of 4μ , the osmiophily disappears and further growth stops. In centrifuged eggs, the dictyoles and young dictyosomes are accumulated in the zone of hyaloplasm,

whereas in the centrifugal yolk zone besides mature granules only transitional stages with little Golgi substance left may be found.

The β -granules are to be considered as reserve proteins. These belong to a group of proteins with a high tendency to crystallization. They mostly form spherical or polyedric bodies; by their ability of swelling and their affinity to plasm stains they differ from true crystals. Sedimentation experiments with the ultracentrifuge have shown that these proteins form spherical macromolecules, as contrasted with the chain molecules of the scleroproteins. According to ASTBURY (1933) and WRINCH (1941) the polymer chains close into rings. This explains why the reserve proteins usually collect into isodiametric bodies. That the shape of the granule is not exclusively determined by the spherical shape of the Golgi body in which it is formed, but is due to the structural forces of the protein itself, may be deduced from those cases, where the Golgi substance forms only a band- or caplike appendage to the granula, while the latter grows at its free surface. The Golgi substance itself contains a protein component; after extraction of the lipids it stains with plasm stains, e.g. with "duroechtred-azure" after fixation in LENHOSSEK's or ROMEIS' fluid, whereby both the dictyoles and the osmiophil outer parts of the dictyosomes stain intensively with azure. AVEL (1925) could stain already the Golgi substance in the egg cell of *Planorbis* with acid fuchsin, crystal violet or iron haematoxylin.

8. MITOCHONDRIA AND ALPHA-GRANULES

The mitochondria and the α -granules which are derived from them (RAVEN and BRETSCHNEIDER 1942) could be demonstrated in the growing oocytes after fixation in lipid-preserving fluids (REGAUD, FLEMMING, NASSANOV, POLL's formol-osmium) and staining with iron



Fig. 12. Transformation of mitochondria into α -granules

haematoxylin or ALTMANN's fuchsin. In the early oocyte the mitochondria are predominantly granular; in later stages more and more filiform mitochondria appear, as thin threads with a length attaining 3.6μ . At their surface granular swellings of 0.5μ diameter are formed; as a rule, the whole mitochondrion is transformed into a chain of those granules (fig. 12). In this stage the mitochondria break down and the α -granules come to lie freely in the cytoplasm, scattered between the β - and γ -granules like the original mitochondria. In the centrifuged egg, the mitochondria are found in the hyaloplasm, whereas the liberated α -granules have a greater specific gravity and form a special zone at the border of hyaloplasm and yolk.

9. LIPIDS

Whereas part of the cell lipids are bound structurally to the Golgi bodies and mitochondria, the presence of free lipids in the cytoplasm

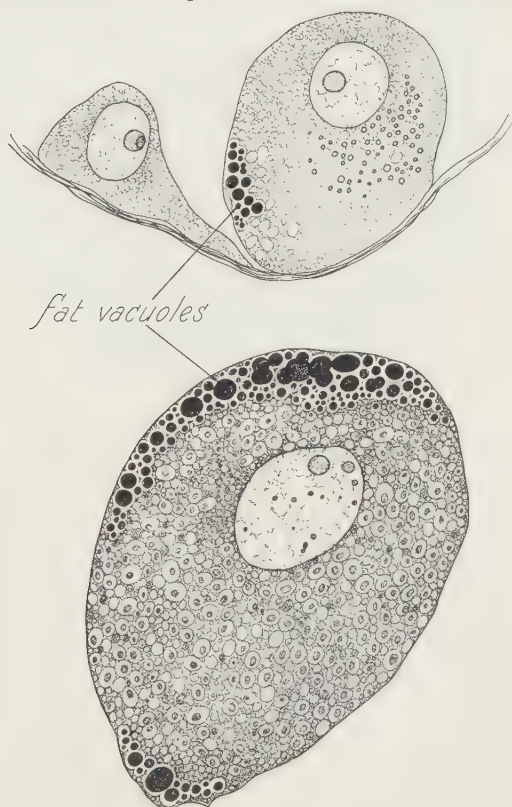


Fig. 13. Formation of fat vacuoles in early oocytes of *Limnaea*

can be demonstrated. After fixation with REGAUD's fluid and staining with iron haematoxylin besides the stained mitochondria and α -granules so-called myelin-negatives are found. With the denaturation of the cytoplasm on fixation twisted figures arise from the mesomorphic lipids which flocculate and form liquid crystals. Such myelin figures are met with likewise with other techniques, e.g. fixation according to ROMELS and azan staining. After CIACCIO's treatment, free cytoplasmic lipids



Fig. 14. Older oocyte with fat vacuoles regularly dispersed through the cytoplasm

surround the fat vacuoles; in centrifuged oocytes, they are lying between these vacuoles in the ground plasm.

Furthermore, the fatty substances of the egg have been studied by staining with Sudan III or Scharlach R after formol fixation; they are found in the oocyte of *Limnaea* as single vacuoles and show no relation to the yolk granules, as in other eggs. The fat arises, mostly peripherally in the hyalin cytoplasm, as a cluster of vacuoles; no visible cell structures preceding their formation have been observed. The first fat vacuoles are formed at the end of the amoeboid phase (fig. 13); from this moment on, their number increases gradually and they are dispersed regularly over the egg (fig. 14). In the full-grown oocyte the fat

occupies about 5 % of the total egg volume. In centrifuged oocytes it accumulates, according to its low specific gravity, as a cap at the centripetal pole (fig. 7, 8).

10. GLYCOGEN

The glycogen has been studied in oocytes, fixed in alcohol, CARNOY or VAN LEEUWEN'S fluid (1 % picric acid in abs. alc. 2; chloroform 2; formalin 40 % 2; glacial acetic acid 1) and embedded in celloidin-

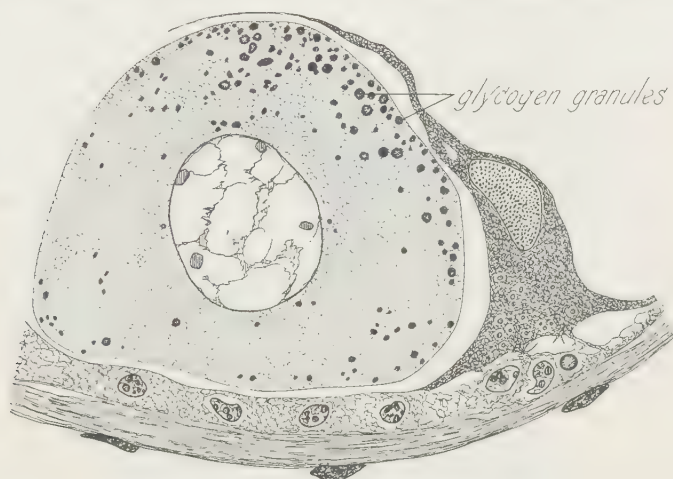


Fig. 15. Glycogen granules in growing oocyte of *Limnaea*

paraffin; staining with BEST'S carmine or with SCHIFF'S reagents according to BAUER; controls have been treated with saliva. The glycogen is not formed in connexion with visible cell structures; as a rule, it is found diffusely in the cytoplasm, only exceptionally in granular form. In the latter case, it seems to accumulate originally in small amounts in vacuoles; gradually its quantity increases until compact granules of variable shapes are formed (fig. 15); they are scattered irregularly throughout the egg. In most cases, moreover a considerable diffuse infiltration of the cytoplasm with glycogen has been observed. The exact determination of its quantity was impossible in consequence of its well-known dispersion during fixation.

11. THYMONUCLEIC ACID

Thymonucleic acid has been studied according to FEULGEN'S technique. The results are rather negative, since a positive reaction has

only been obtained with regard to the oogonium chromosomes at the beginning and the tetrads in the maturation spindle at the end of oogenesis. Already in the ameboid phase the chromosomes are dis-

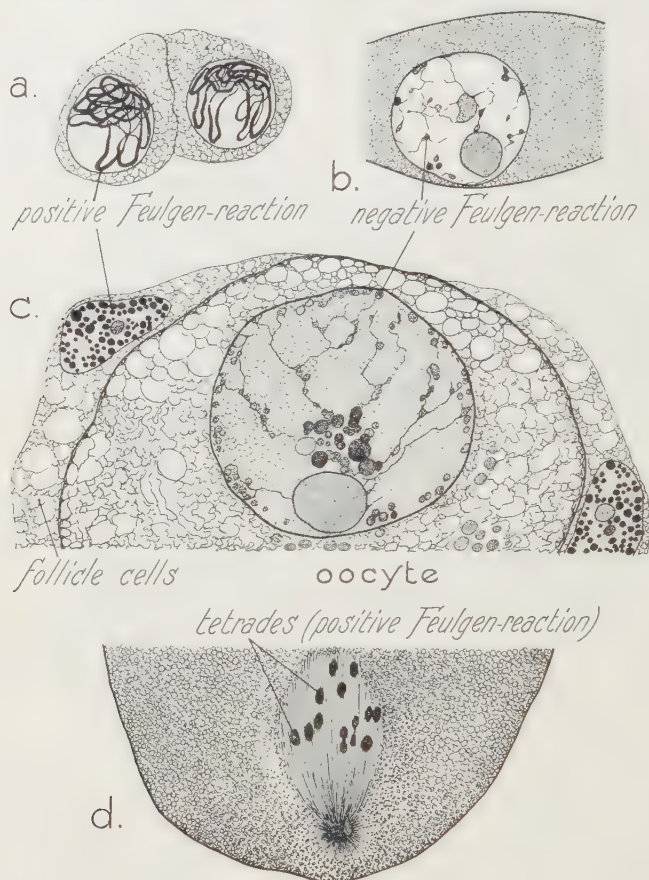


Fig. 16. Feulgen reaction at various stages of oogenesis. a. Oogonia, b. young oocyte, c. full-grown oocyte, d. meiotic phase

persed a great deal and show a negative Feulgen-reaction (fig. 16). This condition, which occurs likewise in other species during oogenesis, remains during the whole period of oocyte development.

12. RIBONUCLEIC ACID

Ribonucleic acid has been determined with BRACHET's (1942) technique: fixation in ZENKER's, HELLY's or BOUIN's fluid, staining with

methylgreen-pyronin and comparison of the stained sections with similar ones which had previously been treated with ribonuclease. From the difference in staining reaction with pyronin between both the localization of the ribonucleic acids in the cell can be derived.

The plasmatic nucleotides are found mainly in a diffuse distribution in the ground plasm. In early amoeboid oocytes their concentration is higher than in older ones; hence, during oogenesis a decrease in the concentration of ribonucleic acids occurs. A close correspondence exists between the basophilia of the cytoplasm after azan staining and the amount of ribonucleic acids. Moreover, the nucleolus contains a great deal of ribonucleic acids; also in this case they are restricted to its basophil parts, whereas the acidophil regions of the nucleolus do not

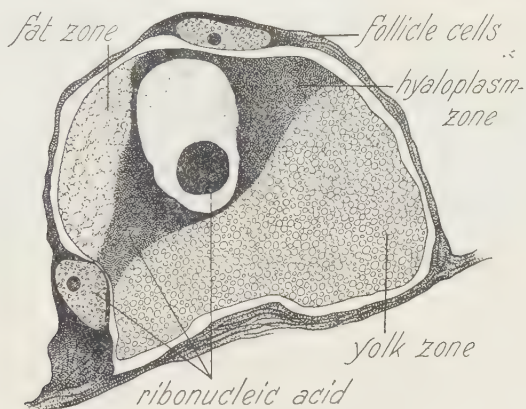


Fig. 17. Centrifuged oocyte of *Limnaea*; Unna. Ribonucleic acid in hyaloplasm and basophil parts of nucleolus; cytoplasm of follicle cells heavily stained

contain these acids (fig. 17). After treatment with ribonuclease the pyroninophily of the cytoplasm disappears altogether, whereas the amphinucleolus retains a weak pyroninophily which is not due to ribonucleic acid. In centrifuged oocytes the pyronin staining caused by ribonucleic acid is restricted to the hyaloplasm and the nucleolus. This does not agree with the results of RAVEN (1945) in freshly-laid eggs, where part of the ribonucleic acid is bound to the β -granules. Apparently, during the passage of the eggs through the oviduct a change in the localization of these acids occurs. Unpublished observations of PH. D. J. W. SEDEE indicate that this takes place in the pars contorta of the oviduct, while the eggs are capsulated in the haustria of this part. This point needs further study.

The diffuse localization of the ribonucleic acids prevents their quantitative determination.

13. GLUTATHIONE

After fixation in BOUIN's fluid the sulphydryl group of the reduced glutathione has been demonstrated according to CHÈVREMONT and FRÉDÉRIC (1943). The distribution of this compound almost corresponds to that of the cytoplasmic nucleotides; it is found diffusely in the ground plasm and in the nucleolus. Likewise, in early amoeboid oocytes its concentration is higher than in older ones. Contrary to the ribonucleic acids, the glutathione is found, however, in the whole nucleolus including its acidophil parts; an emission of glutathione from the nu-

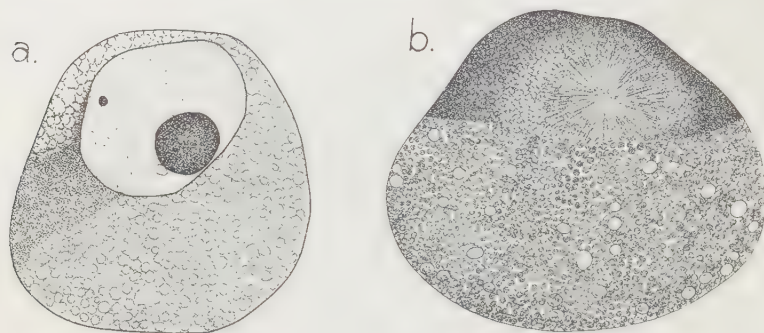


Fig. 18. Centrifuged oocytes of *Limnaea*. a. before, b. after dissolution of germinal vesicle. Staining according to Chèvremont and Frédéric (1943). Glutathione in hyaloplasm and nucleolus; after dissolution of germinal vesicle in cytoplasm around spindle

cleolus to the karyolymph is indicated in many cases. When the nuclear membrane of the germinal vesicle is dissolved in the fertilization phase, the nuclear glutathione spreads through the cytoplasm, and accumulates especially around the maturation spindle and asters (fig. 18). However, already prior to this phase glutathione seems to pass from the nucleus to the cytoplasm through the nuclear membrane.

Since oocytes of equal size may show great differences in amount of glutathione, the synthesis and consumption of this compound during oogenesis seems to occur rather irregularly. In strongly centrifuged oocytes the glutathione is accumulated at the boundary of hyaloplasm and yolk.

14. INDOPHENOL OXIDASE

The indophenol oxidase reaction, carried out in unfixed oocytes with α -naphthol and dimethyl-paraphenyldiamine, presents itself in the form of little granules, which are found already at an early stage as a

little group in the cytoplasm in the neighbourhood of the Golgi field (fig. 19). In full-grown oocytes the granules are dispersed in small groups of 2-5 along the periphery of the egg (fig. 20). The same distri-



Fig. 19. Indophenol oxidase reaction in early oocytes and follicle cells of *Limnaea*



Fig. 20. Indophenol oxidase reaction in full-grown oocyte of *Limnaea*

bution is met with after oviposition. In centrifuged oocytes their specific gravity agrees with that of the hyaloplasm, in which they form a broad band. The appearance of these granules in the neighbourhood of nucleus and Golgi field, simultaneously with the beginning of vitellogenesis, suggests a causal relationship between both. The follicle cells, in which certainly metabolic processes take place in connexion with the nutrition of the egg, are likewise characterized by a large amount of indophenol blue granules.

However, in the early oocytes the cytoplasm surrounding these granules shows a weak indophenol blue reaction, too. This might be explained by an extension of the oxidative action of the enzyme granules to the surrounding cytoplasm. On the other hand, however, it is possible that the indophenol blue is primarily formed diffusely in the cytoplasm, and only secondarily accumulates in the granules.

15. VITAMIN C

Ascorbic acid, demonstrated with acidulated silver nitrate according to GIROUD and LEBLOND, is found in the oocytes in a small quantity only in its reduced form. It presents itself in the form of small granules, either

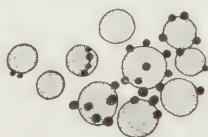


Fig. 21. Vitamin-C granules at the surface of yolk-granules

freely in the cytoplasm or bound to the Golgi bodies (fig. 21). In centrifuged oocytes the free granules are found between the fat vacuoles, the granules bound to Golgi bodies in the yolk zone.

16. IRON

The free ionic iron in the oocyte was determined according to TARTAKOWSKI after fixation with alcoholic ammonium sulphide, staining with potassium ferrocyanide and following treatment with HCl. The cytoplasm of the early amoeboid oocyte is still wholly iron-free. Only with the formation of the follicle the substance appears in a finely granular form diffusely in the perinuclear plasm. In the older stages of the growing oocytes it may be present likewise in this form; a broad peripheral zone of the cytoplasm remains free of iron. Moreover, in most oocytes iron is found in the form of coarser granules in the cytoplasm, the dictyoles and dictyosomes. In the latter, its localisation corresponds,

more or less, to that of the osmiophil Golgi substance; the same appearances of rings, granules, and caps at the surface of the growing beta- and gamma-granules as with osmium impregnation may be observed after precipitation of the iron. Likewise, the dictyoles are wholly impregnated with iron; during their growth, also in this case the centre of the granule appears as a clear internum (fig. 22). According as the beta- and gamma-granules grow older, they stain in a pale blue colour; hence, they contain considerably less iron. Finally, also this last remainder disappears and the granules now take the red counterstain of the eosin.

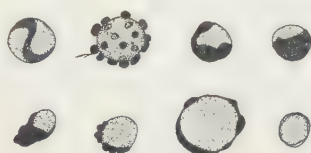


Fig. 22. Localization of iron in the dictyosomes of the growing oocyte

Besides the cytoplasm and the granules, also the nucleolus possesses free iron. In the early oocyte, in which the cytoplasm does not yet show the reaction, already all degrees of iron content, from entirely iron-free nucleoli to those containing a great deal of the substance, are met with. As a rule, it is the basophil part of the nucleolus that exhibits the reaction either in a diffuse or a granular form, whereas isochromatic nucleoli are either entirely free of iron or homogeneously imbibed with it. In the compound forms of the amphinucleoli only some of the vacuoles or granules contain the substance.

The observation that in the same gonad the amount of free iron in oocytes of equal size varies very much speaks in favour of the supposition that the transition of iron from its free form into a masked one takes place very easily and that fluctuations in the proportions between both forms occur during development. This would explain also that according to ARENDSSEN DE WOLF-EXALTO (1947) in freshly-laid eggs the yolk granules again give a strong iron reaction; unpublished observations of SEDEE show that this is already the case in the eggs passing the pars contorta of the oviduct. Presumably, the disappearance of ionic iron in the yolk granules during oogenesis is due to its binding to other compounds; the reverse process sets in as soon as the eggs are ovulated and their passage through the oviduct begins.

17. PIGMENT

The young oocyte, studied *in vivo*, possesses a transparent cytoplasm. According as the oocytes get more proteid yolk, they become a clear

cadmium yellow, by the appearance of a pigment, which belongs to the group of melanines. This colour becomes more intense with the increase of the yolk. In the centrifuged oocytes it is restricted to the zone of proteid yolk. The pigment is bound homogeneously to the β -granules.

DISCUSSION

I. THE METABOLIC MECHANISM OF THE EGG CELLS

When we consider the body of facts obtained by analysis, the question arises in which way the observed structures and substances are related to the metabolism of the growing egg cell. The cytochemical analysis informed us on the presence of various substances and their distribution in the oocyte. Besides this qualitative inventory, by using the stratifying action of centrifuging with respect to several of these substances also a quantitative analysis could be applied. In the majority of cases, moreover, the first appearance of these cell compounds and their increase or decrease during development could be determined. The simple structure of the early oocyte at the beginning of oogenesis, consisting of cytoplasm, nucleus, Golgi field and mitochondria, may be opposed to the much more complicated substantial and structural diversity of the full-grown egg cell. Both are connected by numerous processes progressing side by side with many interrelations between them. The egg cell, on account of its forced growth and synthesis of reserve substances, is greatly in favour as an object for studying the intermediary metabolism.

Summarizing the analysed structures in their relation to cell metabolism, we may group them according to the following view-points (fig. 23):

1. With the genetic function of the egg cell the nucleotides of the nucleus, as compounds of the euchromatin, are closely connected. The thymonucleic acid could only be demonstrated when visible chromosomes are present, as at the beginning of oogenesis and in the ovulated egg with its tetradic chromosomes just before maturation. These chromosomes, as they appear in the sections, either thread-like as in mitosis or as short tetrads in meiosis, only represent the highly spiralized phases of these structures, however; they can be considered as the vehicles of the gene materials. During interkinesis, a despiralization of the chromosomes occurs and the chromomeres are exposed at the inner side of the nuclear membrane; presumably, part of the genes will intervene, during this period, in the vegetative processes of the cell.

According to FREY WYSSLING (1948), the thymonucleic acid might represent an insulator enveloping the genes during mitosis; on the contrary, CASPERSSON (1940) supposes that it plays an active part in the synthesis of gene materials during the reduplication of the chromosomes. However this may be, evidently by the dispersion of the material during despiralization of the chromosomes the amount of thymonucleic acid sinks beneath the lower limit of cytochemical determination and, thereby, becomes invisible for us. When the chromomeres

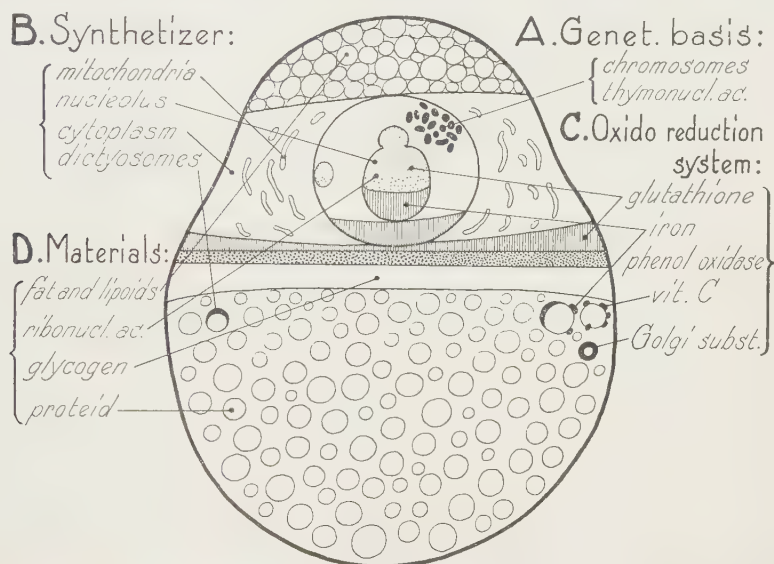


Fig. 23. Diagrammatic representation of a centrifuged oocyte of *Limnaea*, indicating the various structures and substances which may play a part in its metabolism

are again crowded together by the formation of the spiralized chromosomes, the thymonucleic acid appears again. During the vegetative phase of egg growth only thin Feulgen-negative threads may be seen in the nucleus. Before maturation, the strongly condensed gemini and tetrads rather suddenly appear. Hence, in the growing *Limnaea* egg the thymonucleic acid is temporarily lacking or greatly diluted.

2. The oocyte contains a number of universal cell components which are acting as preformed synthetizers. To these belong:

a. The nucleolus. The persisting cunucleolus is a very active vegetative nuclear structure which, apparently, secretes fluid and solid substances in rhythmic succession. Through the nuclear membrane, these substances pass into the cytoplasm. Besides proteins, the nucleolus may produce ribonucleic acid, glutathione and ionic iron; all these substances are found back in the cytoplasm.

From cytological investigations of the past ten years (e.g. CASPERSON, 1940, 1941) it has become evident that basophily is connected with the formation of compounds rich in hexon bases. Especially the histones, with their excess of basic amino-acids, like arginine, contribute to the basophily. They play a large part in the composition of the active nucleolus. As long as no cytoplasmic growth takes place, as in the youngest oocyte, the eunucleolus still consists mostly of proteins poor in bases, but when the oocyte begins to grow the isochromatic structure of the nucleolus changes into that of the amphinucleolus with its pronounced basophily and abundance of histones. Moreover, in the nucleolus of the *Limnaea* oocyte, besides basic proteins and their components, ribonucleic acids, glutathione and iron can be demonstrated; the passage of these substances to the karyolymph is clearly indicated and, at several stages, their transmission from the nucleus to the cytoplasm may be observed¹.

b. The mitochondria, multiplying by division, apparently as lipoprotein synthetizers produce the α -granules.

c. The Golgi elements, present in the early oocyte as single dictyosomes and multiplying by division, as protein synthetizers produce the β - and γ -granules.

Undoubtedly, these three synthetizers take up relatively simple chemical substances and elaborate them to compound substances.

3. The numerous processes of synthesis in the cell take place with the aid of substances that may be taken together as the oxido-reduction system. Among the substances studied by us in the *Limnaea* egg, glutathione, phenol oxidase, vitamin C, the lipoproteids of the Golgi bodies and the iron ion belong to this system.

In connexion with the abundance of yolk of the *Limnaea* egg, protein synthesis takes a predominant place during oogenesis. In the intracellular metabolism and synthesis of proteins the endoenzyme katepsin plays an important part. We cannot make it visible as such by cytochemical methods; glutathione, its zookinase, however, can be demonstrated in this way. We traced it in its reduced form, containing the sulphhydryl group, which is very active chemically; it changes easily into the disulphide compound. Apparently, it is produced in the nucleolus and diffuses through the nuclear membrane to the cytoplasm; especially in the perinuclear plasm it is found in a higher concentration.

Besides katepsin, the cytoplasmic ribonucleic acids play a part in protein synthesis, as has been shown by the researches of CASPERSON, HYDÈN, BRACHET and others. Likewise, these acids are found in the

¹ Since the completion of the manuscript, this metabolic activity of the nucleolus in the *Limnaea* oocyte has been confirmed by ARVY (C. R. Ac. Sci. Paris **228**, 1949).

Limnaea egg both in the nucleolus and the cytoplasm. Especially in the early oocyte their concentration is high; it is probable that the pronounced basophily both of the nucleolus and the cytoplasm in these oocytes depends on their ribonucleic acid content.

Protein synthesis in the growing oocyte involves both cytoplasmic growth and yolk formation. Since the actual processes of synthesis belong to the realm of molecular dimensions, up till now merely single steps of the complicated chain of reactions can be detected. Protein synthesis only becomes visible as soon as it occurs structurally bound to the Golgi bodies as matrices of the β - and γ -granules. The Golgi bodies of the *Limnaea* egg have been described already by GATENBY (1919), but he did not consider them as the moulders of the proteid yolk that was derived by him from the mitochondria. The Golgi substance with its abundance of lipids, containing unsaturated fatty acids, likewise plays a particular role as a hydrogen acceptor and donator. Its reducing action is still reinforced by its narrow connexion with the affixed vitamin C, which is a strongly reducing substance, whereas the iron, as an oxygen carrier, is placed on the oxidative side of this system. Though we could detect only a small amount of ascorbic acid in the *Limnaea* egg, it has to be kept in mind that this substance is very susceptible to oxidation and unstable in the presence of oxygen. Moreover, the glutathione with its sulphydril group may have an inhibiting effect on the vitamin C. The latter may convey its reducing properties to other cell structures, as granules and Golgi bodies, by which it is accumulated.

To re-oxidize the substances reduced in this way stronger oxidizing actions are needed, which are supplied in the living cell especially by the iron ion. A great deal of oxidation processes are catalyzed by iron. Together with vitamin C, the iron may act as an activator of kathepsin. The iron is found in a high concentration in the nucleolus and in the Golgi substance as sites of protein synthesis, in a low concentration and only temporarily in a diffuse form in the cytoplasm.

Besides the presence of lipoproteins the mitochondria up till now show no conspicuous chemical differentiation. They fall apart into α -granules. Both the Golgi bodies and the mitochondria are no stable persistent cell structures but mere optical expressions of a dynamic process; although they are morphologically well-defined structures, they have only an ephemeral existence and are actually of a dynamic nature¹.

The phenol oxidase demonstrated cytochemically in the egg cell may be connected with cellular respiration. The peripheral position of this endoenzyme speaks in favour of this assumption.

¹ PALADE and CLAUDE (J. Morph. **85**, 1949) have shown that many of the morphological features of the Golgi apparatus in fixed cells may be due to fixation artifacts.

4. Finally, a last group is constituted by the energy-producing and building materials. The hyaline ground plasm including the cytoplasmic nucleotides build up the cell body, the nuclear proteins and thymonucleic acid the structures of the nucleus. Cytoplasmic lipids, observed as diffusely dispersed osmiophil substances in the cytoplasm or precipitated as myelin figures, like those described by MONNÉ (1942) in the egg cell of *Helix*, belong to the building materials of the cell body.

Other building materials, as the paraplastic inclusions (e.g. the protein yolk granules) have to do with the future development of the embryo.

Finally, the fatty yolk and glycogen represent the energy sources for the building processes and movements during embryonic development. Both the synthesis of glycogen and fat takes place inconspicuously and is, apparently, not bound to visible structures.

2. THE POLARITY OF THE EGG

In the earliest oocytes, polarity is not yet clearly visible. The nucleus has a position near the centre of the egg cell. The Golgi field is situated near it. Theoretically, a line drawn through the centres of nucleus and Golgi field might represent a leading direction of the cell. There are no indications, however, that it is privileged in any way, e.g. during amoeboid movement. The mitochondria show a regular dispersion through the cytoplasm. The fat vacuoles appear in the periphery of the cytoplasm without any regularity. The first indophenol oxidase granules arise in the neighbourhood of the Golgi field. Soon, the Golgi field disperses into granules which are scattered through the cytoplasm. The first yolk granules are formed in the central part of the egg.

As soon as the oocyte becomes sessile and is enveloped with follicle cells, a clear apico-basal polarity appears. Whereas the basal part of the egg cell borders upon the connective tissue surrounding the gonad, its lateral and apical sides are covered by nutritive cells. The nucleus now takes an eccentric position in the apical half of the oocyte. At the apex hyaloplasm is accumulated during the growth phase, part of which sinks into the depth and forms the perinuclear plasm. In the distribution of the yolk, however, no further indications of a polar differentiation are visible.

When the nuclear membrane dissolves in the full-grown oocyte, the developing maturation spindle is still situated in the apical half of the egg.

After oviposition, the polarity of the egg is very pronounced (RAVEN 1945). The maturation spindle is situated in the animal half, its

longitudinal axis coinciding with the egg axis. At the vegetative pole, a special vegetative pole plasm is accumulated, differing from the rest of the egg in its staining properties and bordered by sharp boundaries. When the egg leaves the gonad after ovulation, this pole plasm has not yet been formed. Hence, its accumulation at the vegetative pole must take place during the passage of the egg through the oviduct. Unpublished observations of SEDEE indicate that this does not occur before the eggs have reached the pars nidamentaria of the oviduct, where the capsulated eggs are united into an egg-mass (BRETSCHNEIDER 1948b).

It may be supposed that the animal-vegetative polarity of the oviposited egg corresponds to the original apico-basal polarity of the growing oocyte. It is difficult to prove this point, however, since ovulation is followed by a new phase of pronounced amoeboid activity while the eggs are in the spermoviduct and the first parts of the oviduct (BRETSCHNEIDER 1948a). During this phase, by the strong distortions which the egg undergoes the nucleus or spindle may be displaced so that no trace of the original polarity remains. Only after the eggs are surrounded by the egg capsule fluid in the haustria of the pars contorta of the oviduct they round off again and the maturation spindle takes its position in the future animal half of the egg.

SUMMARY

1. Oogenesis in *Limnaea stagnalis* has been studied, partly by means of cytochemical methods.
2. Various phases in the development of the egg cell are distinguished; the growth phase is preceded by an amoeboid phase and succeeded by a rest phase prior to ovulation.
3. The cytoplasm increases during growth to 223 times its original volume; its relative amount decreases from 63 % to 40 % of the total egg volume.
4. The nucleus increases during growth to 162 times its initial volume; its relative size decreases from 47 % to 17 % of the total egg volume. Rhythmical pulsations of the nucleus seem to occur during the growth phase.
5. The nucleolus shows a considerable synthetic activity during the growth phase. Both intranucleolar and epinucleolar formation of products take place; the latter are extruded into the karyolymph and may pass the nuclear membrane into the cytoplasm.
6. The proteid yolk consists of 2 kinds of granules of different size and shape (β - and γ -granules). Both are formed by the Golgi bodies.

The latter are at first impregnated as a whole with osmium or silver. Later, a clear centre appears which is the germ of the proteid granule. As this is growing, the osmiophil Golgi substance is more and more reduced.

7. The mitochondria of the egg break down into α -granules.
8. Cytoplasmic lipids and neutral fats appear in the cytoplasm without any relation to visible cell structures.
9. Glycogen is not formed in connexion with visible cell structures, but may originally accumulate in vacuoles.
10. Thymonucleic acid can only be demonstrated in the oogonium chromosomes and the tetrads of the maturation spindle; during the growth phase, the Feulgen reaction is negative.
11. Ribonucleic acid is found in the cytoplasm and the nucleolus. In the cytoplasm, its concentration decreases during the growth phase. In the nucleolus, it is restricted to the basophil parts. During the passage of the eggs through the oviduct the ribonucleic acid is accumulated in the β -granules.
12. Glutathione is found in the cytoplasm and in the nucleolus. Its concentration in the cytoplasm decreases. In the nucleolus it is found both in the acidophil and the basophil parts. After the dissolution of the nuclear membrane, the nuclear glutathione accumulates around the maturation spindle.
13. Indophenol oxidase granules may be demonstrated along the periphery of the egg. They first appear in the neighbourhood of the Golgi field.
14. Vitamin C is present in a small quantity in the cytoplasm and the Golgi bodies.
15. Ionic iron first appears in the perinuclear plasm. Later, it is found in the cytoplasm and the Golgi bodies. During the passage of the eggs through the oviduct it appears in the β -granules.
16. A yellow pigment is bound to the yolk granules.
17. The earliest oocytes possess no distinct polarity. During the growth phase a clear apico-basal polarity is indicated by the position of the nucleus and the perinuclear plasm. After ovulation the polarity is not clearly visible in the amoeboid eggs. The oviposited eggs show a distinct animal-vegetative polarity, with a well-developed vegetative pole plasm. The latter does not arise before the eggs have reached the pars nidamentaria of the oviduct.
18. The role of the various components of the egg cell with respect to its metabolic mechanism is discussed.

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THE SHELL OF *OSTREA EDULIS* AS A HABITAT

OBSERVATIONS ON THE EPIFAUNA OF OYSTERS LIVING IN THE
OOSTERSCHELDE, HOLLAND, WITH SOME NOTES ON
POLYCHAETE WORMS OCCURRING THERE IN OTHER HABITATS

by

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INTRODUCTION

In the course of extensive investigations on shell disease in *Ostrea edulis*, I gradually managed to discover the uniformities in the epidemiology of this once so mysterious plague. In the year 1940 I realised that this disease claims new victims during hot spells only. Much later I was able to say that a new wave of infection does not start before there has been a 10-days period with water temperatures of 19° C. or higher. After that young oysters are liable to become affected by shell disease so long as the water temperature remains at or above 19° C. The higher the temperature, the more vigorous the attack.

Further it could be demonstrated that the intensity of the attack differs greatly from place to place. By charting the data collected in several years, different foci of shell disease could be pointed out.

A lack of knowledge of the true character of the disease, the predominating influence in its spread of the factors of water temperature and position, and the apparent unimportance of the kind of collector used for the young oysters under consideration, led me to wonder whether or not an animal vector could be held responsible for carrying this disease. I therefore decided to carry through a survey of the animals closely associated with the oyster throughout the summer season. In this, special attention has been paid to a station at Yerseke, where the disease appeared to rage more violently than anywhere else in the Oosterschelde. Some preliminary observations were made in the year

1940. A more detailed and quantitative study has been carried out in the summer seasons of the years 1941 to 1945 inclusive.

Though investigations carried out along different lines eventually contradicted the hypothesis that animal vectors were involved in carrying shell disease, I consider the observations made and the data collected on animals associated with oysters too interesting from a general zoological point of view to keep them in the dark.

Hence this paper.

Though the oyster beds in the Oosterschelde are thoroughly and regularly cleaned by heavy dredges, and though the oysters grown there pass the hands of oystermen several times before they are marketed, a surprisingly rich fauna appears to be associated with oysters.

Well-kept oyster beds are nearly as poor in species of "vermin" and "weeds" compared with untouched natural oyster beds, as well-cultivated arable soil is compared with marshes and wasteland. The shells of the Dutch oysters, nevertheless, appear to lodge a rich and fascinating fauna.

ACKNOWLEDGEMENTS

A great number of species, belonging to several phyla of invertebrate animals, was found to inhabit the oyster's shell. I did not try to identify all the species collected myself. I concentrated on the Polychaete worms, which usually predominated both in number and variety in this very special habitat. In studying this most interesting group, I received valuable assistance from Miss A. P. C. DE VOS of the Amsterdam Zoological Museum, and from Prof. P. FAUVEL, the famous French authority on Polychaete worms, who was so kind as to check some difficult identifications.

The following Dutch specialists have been kind enough to undertake the identification of animals belonging to several other groups of invertebrates. Dr W. VERVOORT (Mus. Nat. Hist., Leyden) identified Ascidians, Porifera, Hydrozoa, and Bryozoa; Dr J. H. SCHUURMANS STEKHOVEN Jr. (Zool. Lab., Utrecht) studied the Nematode worms I collected on the shells of oysters. Without my knowledge he published an account of his findings (1941). Though he had been informed of the provenance of this material, he erroneously stated that the Nematodes under consideration had been found inside the oyster's shell cavity, and in this connection speculated on their possible influence on the oyster's well-being. Miss A. P. C. DE VOS (Zool. Mus., Amsterdam) identified the Oligochaete worms, and the Harpacticid Copepods. Her findings on the latter group have been published in this journal (1945). The late Dr H. C. REDEKE identified the Ostracods, Dr K. SCHIJFMA (Mus.

Nat. Hist., Leyden) the Amphipod Crustaceans, and Dr L. B. HOLT-HUIS (Mus. Nat Hist., Leyden) the Decapod Crustaceans. The late miss A. M. BUITENDIJK (Mus. Nat Hist., Leyden) was kind enough to identify both Cumaceans and Pycnogonids. Mrs. VANDER FEEN, nee VAN BENTHEM JUTTING (Zool. Mus., Amsterdam) studied the juvenile Lamellibranch Molluscs, and Dr H. ENGEL (Zool. Mus., Amsterdam) the Nudibranch Gastropods and the Echinoderms found on the oysters.

In later years I could easily identify the predominant species myself, having properly identified material close at hand.

I wish to express my sincere gratitude to the aforementioned biologists for the identification of the material discussed below.

It is a pleasure to thank miss S. M. Marshall of the Scottish Marine Biological Station at Millport for her kindness to correct the English text of this paper.

THE SHELL OF THE OYSTER AS A HABITAT

It is amazing that little attention has been paid thus far to the epifauna of the oyster. MOEBIUS (1893) studied the animal communities occurring on the German oyster beds, which ultimately led him to formulate the now well-known concept "biocoenosis". Oysters being rather scarce on these natural beds, far more attention was paid to the creatures found in between the oysters – either living freely in water and sediments, or attached to stones and other supports – than to those using the shell of the living oysters as a habitat.

The same can be said of the section of ZERNOV's paper (1913), which deals with the natural oyster beds of the Black Sea, and of the section on oyster beds in VERRILL's paper (1873) on Vineyard Sound (Mass., U.S.A.). MIYAZAKI (1938) made a study of the organisms fouling the shell-strings hung from rafts in some Japanese oyster-farms. Several of these creatures are considered as competitors with the oyster for food and space. Moreover they compel the oystermen to go to considerable trouble and expense to clean spat and oysters before these can be sold. Some observations have been made on the season of attachment of the fouling organisms in these Japanese oyster-farms. No special attention has been paid by MIYAZAKI to the small and often non-sedentary creatures, which use the shell of the oyster more or less exclusively as a habitat. SCHODDUYN (1927) deals with the fauna of an oyster basin of rather primitive construction near Boulogne-sur-Mer (Pas-de-Calais, France), and so does FERRONIERES (1901) for oyster parks near le Croisic (Loire Inférieure, France). This is in line with LELOUP's paper (1940) on the flora and fauna of the Bassin-de-Chasse (Ostend, Belgium), in which oysters are kept. The data from the last three papers

are interesting for the sake of comparing the fauna of oyster parks and basins in France and Belgium with that in the Oosterschelde (Holland), but give little information on the animals living on and in the oyster's shell.

As far as I am aware, only SCHODDUYN's 1931 paper deals especially with the organisms found on the shells of living oysters. The oysters investigated by him were market oysters, however, temporarily stored in a basin. They had undergone a thorough scrubbing, hosing and washing, and often had been transported over considerable distances before SCHODDUYN got hold of them and could investigate their occupants. He therefore often detected little more than debris and remains of the interesting epifauna of the oyster.

In his study on the damage done by the flatworm *Stylochus pilidium* (GOETTE), BYTINSKI-SALZ (1935) makes some remarks on the epifauna of the oysters suspended in an oyster park near Rovigno d'Istria. In addition to sedentary organisms such as Algae, Hydroids, and Bryozoa, he found both Polychaete worms and the Decapods *Pilumnus hirtellus* (L.) and *Porcellana longicornis* (L.) in great numbers on the shells of his oysters.

Both sedentary and free-living animals can be encountered on the oyster's shell. Though many of the former are also found on other substrata, several of the latter are more or less characteristic of the shells of living oysters, and are but rarely encountered outside this habitat. A short list of the more numerous and conspicuous Polychaete worms living on oyster shells and those living in the superficial layers of the oyster bed suffices to support this statement: TABLE I (See page 36).

Though the value of this list should not be overemphasized, as it is a matter of course that burrowing forms will feel more at home in sediments than on oyster shells, it is enough to demonstrate that several species are conspicuously abundant on shells of living oysters. Apparently the micro-ecological conditions prevailing there appeal to many creatures. Next to some incidental guests many species occur here so regularly, that we may speak of the biocoenosis of the shell of the oyster. It need not surprise us that the exploration of this so far little known habitat led to the finding of many species until now unknown from the Dutch coast. Apart from the fact that Polychaete worms have received too little attention from Dutch biologists up till now, the investigation of a new type of habitat always leads to the finding of animals considered rare or missing in the local fauna up to that moment. Though BAAS BECKING's (1934) verdict "everything is everywhere, the milieu selects" and the saying of an old Dutch entomologist "rare

TABLE I

Polycheate worms found on shells of living oysters and on the oyster beds of the Oosterschelde

+ = present, but rare; ++ = common; +++ = abundant

	on oysters	on oyster beds
<i>Lepidonotus squamatus</i>	++	+
<i>Harmothoë imbricata</i>	+	+++
<i>Harmothoë impar</i>	+++	++
<i>Pholoë minuta</i>	+++	+
<i>Eulalia viridis</i>	++	+
<i>Eulalia sanguinea</i>	++	+
<i>Phyllodoce maculata</i>	++	++
<i>Eteone picta</i>	++	+
<i>Autolytus aurantiacus</i>	+++	—
<i>Autolytus cornutus</i>	+	—
<i>Nereis succinea</i>	+	+++
<i>Platynereis Dumerilii</i>	++	++
<i>Polydora ciliata</i>	+++	++
<i>Nereis diversicolor</i>	—	++
<i>Arenicola marina</i> (adult)	—	++
<i>Scoloplos armiger</i>	—	+++
<i>Nephtys Hombergi</i>	—	++
<i>Tharyx multibranchiis</i>	—	++
<i>Heteromastus filiformis</i>	—	++

animals do not exist, the point is where to look for them" certainly are somewhat exaggerated and provoke contradiction they have a kernel of truth.

Those who are extremely keen on the finding of new records for the national fauna, should be well aware that the species listed in this paper do not necessarily belong to the autochthonic fauna of the Dutch inshore waters. Though I feel sure that the vast majority of the animals found on the shells of living oysters have occurred here on natural oyster beds since time immemorial, with some obvious and well-known exceptions (e.g. *Crepidula fornicata* (L.)), it is possible that some species have been introduced accidentally from abroad. Sometimes the Dutch oystermen scattered young French oysters on their beds to replenish their depleted stocks. This was done after the devastating winter of 1890-91 and again on larger or smaller scale in the years 1936, 1937, 1938, 1939, 1940, 1944, 1946, 1947, 1948, 1949. Though the French oysters, purchased in the Morbihan (Brittany) and in Arcachon (Gironde) are usually very

clean indeed, and though few animals living on the oyster's shells will survive the journey, some may. Often species thus introduced from abroad cannot survive and/or reproduce in the new environment, especially because of lower temperatures in summer and/or winter, compared with the waters they came from. Some may feel at home, however. I feel sure that at least a few of the species mentioned below have been introduced with French oysters, but it will be very difficult indeed to adduce convincing evidence in any particular case whether a species should be reckoned to belong to the original fauna of the Oosterschelde. The specimens discussed in this paper have all been found on the shells of native Dutch oysters, and therefore are at most descendants of new-comers from abroad and in no case the introduced specimens themselves.

Noting the great number of species occurring on the shells of living oysters, we wonder what micro-ecological conditions render these shells so attractive as a habitat. Since the oysters live below low water level in the Oosterschelde, there is no reason to assume that water temperature, salinity or pH differ noticeably from those prevailing in the bulk of the sea-water. Though I admit that these factors are very important in ecology, I feel that the ease with which they can be measured often leads to serious undervaluation of the importance of other ecological factors. In the special case of the shell of the oyster as a habitat, the factor "shelter" is probably of great importance.

The oyster shell offers excellent hiding places, even to fairly large animals. In this the flat valve is of greater importance than the cupped one. On the flat shell concentric rows of fairly large imbricate scales, (this is the prismatic layer of the oyster shell, present on the flat valve only) offer an excellent opportunity for hiding or for making either a temporary or a permanent burrow. By placing the oysters in a shallow dish with sea-water, and by lifting the scales of the prismatic layer one by one with a preparation needle, we can collect the many denizens of this very special habitat. Though the majority of the non-sedentary animals living on the shell of the oyster is to be found on the flat valve, the number living on the outside of the cupped shell is by no means unimportant. Depending on ecological conditions, especially on currents and wave-action, the cupped valve is more or less ribbed, and these ribs are more or less fluted. Thus many a fine shelter is available to the members of the epifauna. Both on flat and cupped valves the oyster's epifauna finds plenty of opportunity to burrow and to hide out of sight and out of reach of their predators.

Another important side of the factor "shelter" no doubt is protection from silting. Pebbles and shells lying on the bottom of the sea, and

especially in estuaries, are always liable to gradual silting or to becoming covered by fine sand. Then the epifauna on such a substratum faces disaster. A living oyster, on the other hand, usually manages to keep reasonably free from silt and sand, which means permanent protection from this danger to its epifauna.

We wonder whether the factor food shows special features on the shell of the oyster. Unfortunately we know very little about the feeding habits of the different animals encountered there. A tentative classification, based on the type of food used, has been made for Polychaete worms (VON BRAND, 1927), but in too few species have we knowledge of their daily diet. The vast majority of the data in the literature is of a purely taxonomic and faunistic character.

There is ample evidence that very many members of the community found on the oyster's shells do not use the shell as a temporary shelter only, but are more or less permanent residents. We might suppose that the non-sedentary species leave the oyster at night, to hunt for food, and return to their appropriate shelter later. I examined many oysters, however, which lived in wire-covered trays, and was able to compare them with oysters living on the oyster beds. There appeared to be no significant difference in epifauna. If the animals really left the oyster at night, it would be far more difficult for them to find the oysters in the trays again, than oysters living on the beds. In that case we should expect a far poorer epifauna on oysters kept in trays. This is not the case, however. Oysters in trays usually display a richer epifauna than those lying on the beds.

As will be demonstrated below, the majority of the members of the epifauna do not reach the oysters during rambles on the sea-bottom, but settle down on the oyster's shell at the moment they end their planktonic life. There is little doubt that many members of the oyster's epifauna find their food on the shell itself. Both microscopic and macroscopic plants live on and in the shell, protected from silting, and may serve as food to many animals. Other members of the epifauna are able to collect their food from the surrounding sea-water, or can utilize the particles of detritus deposited on the shell. Several others are predatory on those herbivores, filter-feeders, and detritus collectors. Unfortunately I must leave undecided to which category belongs every separate member of the rich epifauna of the oyster's shells.

We wonder whether or not the oyster itself contributes to the food of its epifauna. Though I investigated this possibility very carefully, I found no evidence that any of the epibionts can be considered as true parasites feeding on the living tissues of the oyster itself. The possibility remains, however, that faeces and pseudo-faeces (dejecta and rejecta) produced by the oyster may contribute to the fertility of the habitat.

Pseudofaeces and faeces mainly consist of material concentrated by the oyster from the surrounding sea-water by means of its intricate and efficient filtering apparatus, and are rich in organic material. At least part of this material may become deposited on the shell of the oyster, especially if large numbers of oysters are kept on trays. In an effort to investigate this matter, I made a lot of "dummy" oysters by gluing together empty shells of oysters of comparable shape, texture and size. I exposed those dummy oysters for prolonged periods on trays in the station where I kept my living experimental oysters. I compared the epifauna of the living oysters with that of the dummy's. Contrary to expectations no difference of any importance has been found in the number of species and individuals inhabiting the shells of living and dummy oysters: TABLE II (See page 40).

From this evidence we can draw the conclusion that the production and deposition of faeces and pseudofaeces by the oyster itself is not a factor of great importance in the ecology of the epifauna of the oyster shell.

QUANTITATIVE DATA

As mentioned above, the primary purpose of my observations on the epifauna of the oyster was to find out whether or not the marked periodicity in the spreading of shell disease was accompanied or preceded by a similar periodicity in the occurrence of one or more of the animals associated with the oyster. To this end series of quantitative observations, made at frequent intervals, were started. This was carried on for several years in succession, especially because the data collected in the first summer (1941) seemed to support my hypothesis that an animal vector is involved in the spreading of shell disease.

From a general zoological point of view the quantitative data collected are highly interesting, because they clearly demonstrate how the little community on the shell of the oyster develops gradually in the course of the year. Experimental oysters, all of the same age-class, and approximately of the same size, were kept on wire-covered trays in exactly the same position every year, and placed and kept there in exactly the same way.

In the course of the season more and more creatures settle down on the shells, while others disappear from the scene as the season advances.

A complication is that the size of the oysters, and with that the surface area of their shells, increases as the oysters grow in the summer season. In my well-selected station at Yerseke I placed every year trays with young oysters (10 months old), newly detached from tile-collectors, and practically without epifauna. Roughly speaking we can

TABLE II

Yerseke 1942. Epifauna of living oysters from regular series,
compared with that of dummy oysters

Material	50 oysters regular series. Born 1940. Diam. 55 mm	50 oysters regular series. Born 1941. Diam. 35 mm	50 dummy oysters diam. 45 mm	50 oysters regular series. Born 1941. Diam. 52 mm	50 dummy oysters diam. 45 mm	50 oysters regular series. Born 1941. Diam. 56 mm	50 dummy oysters diam. 45 mm
Period of exposure	4-6-1942- 20-7-1942	4-6-1942- 20-7-1942	12-6-'42- 20-7-1942	4-6-1942- 1-9-1942	12-6-'42- 1-9-1942	4-6-1942- 8-9-1942	12-6-'42- 8-9-1942
Foraminifera:							
<i>Crithionina heinckei</i>	++	++	+	++	++	++	+
Ciliata:							
<i>Folliculina ampulla</i>	++	++	++	+++	+++	+++	+++
Porifera:							
<i>Haliclone limbata</i>	+	—	—	+	—	++	—
Coelenterata:							
<i>Laomedea loveni</i>	+	—	—	—	—	—	—
<i>Aurelia aurita</i>	++	+	+	++	+++	++	+++
<i>Sagartia anguicoma</i>	—	—	—	+	—	+	—
Nematoda	2	4	—	1	—	1	—
Polychaeta:							
<i>Lepidonotus squamatus</i>	18	5	2	6	4	1	13
<i>Harmothoe impar</i>	94	26	30	100	26	124	28
<i>Pholoe minuta</i>	65	39	50	60	86	58	67
<i>Phyllodoce maculata</i>	5	1	4	—	2	1	—
<i>Eulalia viridis</i>	—	1	—	—	—	—	—
<i>Eulalia sanguinea</i>	46	9	24	6	2	11	3
<i>Autolytus aurantiacus</i>	60	27	44	9	6	18	2
<i>Nereis succinea</i>	—	—	—	—	—	1	—
<i>Polydora ciliata</i>	40	36	36	34	6	37	2
Ostracoda:							
<i>Luxoconcha impressa</i>	—	—	—	2	—	—	—
Harpacticida:							
<i>Longipedia minor</i>	+	++	+	+	+	+	—
Aphipoda:							
<i>Corophium acherusicum</i>	3	—	—	—	4	3	3
<i>Microdeutopsis gryllotalpa</i>	—	—	—	2	—	1	—
Decapoda:							
<i>Carcinides maenas</i>	8 juv.	7 juv.	—	7 juv.	—	3 juv.	—
Pycnogonida:							
<i>Anoplodactylus petiolatus</i>	—	—	—	—	—	1	—
Bryozoa:							
<i>Bugula plumosa</i>	—	+	—	—	—	+	—
<i>Barentsia gracilis</i>	+	+	—	—	—	—	—

say that the diameter of their shell increases so long as the temperature of the water remains above 15° C. Besides these I often placed oysters one year older (22 months) on a tray in the same station, and made observations on their epifauna at frequent intervals. The area of the shells of these oysters increased also as their shells put on new growth. Expressed as a percentage of the original shell area, increase of available space remained far behind that in the younger oysters.

The new-comers on the shell of the oyster are practically always of a very small size, but occasionally larger specimens make a sudden appearance. The latter should be considered as incidental visitors and seldom remain. They can hardly be reckoned to belong to the characteristic epifauna of the oyster shell. The true members of the bio-coenosis of this habitat settle down there as young individuals coming from the plankton.

An interesting experiment adduced evidence to support this view. In the very same station at Yerseke where I placed my trays with oysters, I placed a row of wooden boxes, measuring $50 \times 50 \times 20$ cm.

Two of the side-walls and the bottom of those boxes consisted of monel metal wire netting with different sizes of mesh. Every box was placed with its corners on 4 concrete blocks ($20 \times 20 \times 20$ cm) and was thus kept well above the bottom. Inside the boxes I placed about 50 young oysters. The lids of the boxes were well fitted against the walls with the aid of rubber tubing and clasps, so that sea-water and animals could enter only through the meshes of the wire netting. I cleaned the wire once every week, so that oysters and epifauna could not suffocate by a possible smothering of the wire netting. Even so, the boxes with closely woven netting showed a poorer growth of the oysters, which indicates that smaller quantities of water flowed through those boxes. The boxes with coarse mesh, on the other hand, had an ample sea-water supply from the tidal current. At the end of the season I collected the animals present in the boxes and on the oysters, which animals must have arrived there through the meshes of the netting. Many of the specimens collected were now unable to leave the boxes in the same way, because of their size. This proves that they must have entered the boxes as tiny specimens. In table III the results of these observations have been tabulated. Even through netting with 80 meshes/inch an appreciable number of members of the oyster's epifauna could make their entry. Some species, however, are decidedly more numerous in the boxes with the coarser netting. I must leave undecided whether this should be ascribed to a reluctance or inability of the early sedentary phases to enter through the finer meshes or to a poorer aeration and nutrition in the boxes with closely woven netting.

TABLE III

Yerseke, 1940. Epifauna of oysters placed in wooden boxes fitted with wire netting

Mesher per inch	3	5	10	18	30	40	50	80
Polychaeta:								
<i>Lepidonotus squamatus</i> .	—	2	2	7	2	1	—	—
<i>Harmothoë imbricata</i>	—	1	3	2	—	—	—	—
<i>Harmothoë impar</i>	18	20	15	30	20	21	25	—
<i>Pholoë minuta</i>	40	50	40	75	40	38	20	15
<i>Phyllodoce maculata</i>	—	—	—	1	—	—	—	—
<i>Eulalia viridis</i>	1	3	—	—	—	5	1	—
<i>Eulalia sanguinea</i>	16	12	10	3	6	5	10	15
<i>Eteone picta</i>	6	14	8	4	2	—	2	1
<i>Autolulus aurantiacus</i>	15	10	25	15	1	—	1	1
<i>Nereis succinea</i>	—	—	1	3	—	—	—	—
<i>Platynereis Dumerilii</i>	15	5	4	8	2	1	—	2
<i>Polydora ciliata</i>	32	20	20	10	25	60	25	10
<i>Capitella capitata</i>	—	—	—	—	—	1	—	—
<i>Lanice conchilega</i>	1	—	—	1	—	—	—	—
Oligochaeta:								
<i>Peloscölex benedeni</i>	—	—	2	—	—	—	—	—
Mollusca:								
<i>Tapes pullastra</i>	—	—	+	—	—	—	—	—

In the station used (Yerseke, "Kijk-uit") the oysters have been kept on trays measuring $200 \times 100 \times 8$ cm. The sides of the trays consisted of wood, the bottom of wire netting with square meshes, 3 per inch, and galvanised before and after weaving. All trays were treated thoroughly with coaltar to prevent corrosion and attack by shipworms. The trays were placed on 6 concrete blocks ($20 \times 20 \times 20$ cm) and covered by a lid of exactly the same construction, and kept in place with large iron hooks driven into the bottom. In the course of the season the meshes of the lid gradually clogged up with algal growth. An adequate renewal of water, and thereby a regular supply of food was ensured through the meshes of the lower tray, which did not foul to any extent. Weekly samples of oysters were taken out of the trays for investigation in the laboratory. Here the oysters were placed in shallow dishes with sea-water. The scales of the flat valves were lifted one by one to collect the epibionts hiding there. Further I poked into all the pits and shelters of the cupped valves to look for additional animal denizens. A needle, a pipette and a binocular lens were the main tools used. In my series of

samples I usually investigated 50 oysters. If samples are wrapped in paraffine-coated paper, and put in a cool place, they can be kept overnight without significant losses among the epibionts.

Though I studied qualitatively the epifauna of oysters taken from many different beds, my quantitative samples all come from the same station "Kijk-uit", Yerseke, selected because of its serious infection with shell disease. This station is a tidal basin, situated a few hundred yards north of the harbour of Yerseke. Tidal basins are pieces of tidal flats enclosed by low dikes, so that they remain permanently filled with sea-water. The dikes emerge a few hours before low tide, and become covered with water with the rising of the flood. The oystermen use tidal basins for the storage of oysters, tile-collectors bearing oyster-spat, and trays with recently detached spat. Some tidal basins are constructed free on the tidal flats, others are built against a big and high sea-dike. Our basin belongs to the latter category. It measures 40×50 metres, and its western side consists of the dike of the Buren-polder, several metres high. The bottom of this tidal basin consists for the greater part of a mixture of mud, sand, old shells and pieces of old broken tile-collectors. Less than 30% of the material of the superficial layers was found to be sand and mud. Therefore it can be said that the basin has a very firm bottom. The low dikes enclosing the basin on three sides are 110 cm high, a sluice-gate, constructed in the middle of the eastern side, is 100 cm high, so that the basin remains filled with water to a depth of 100 cm at low tide. As the bottom of the basin is situated about level with the average low tide, it is covered with more than 3 metres of water at high tide. The oysters were kept on trays, placed about 20 cm above the bottom. In order to take samples and to inspect the trays I opened the sluice-gate until the water was about level with the lids of the trays. Thus the oysters were never fully exposed to the air. A few hours later the incoming tide restored the original water level. Tidal currents sweep rather violently over the basin and bring such an abundance of food that oysters grow exceptionally well in this basin.

Considering the hydrographical conditions prevailing there, we might consider it as an artificially elevated piece of sea-bottom, always covered with water, and still easy to reach at low tide, unless strong western winds prevent the tide from going out normally. Such a basin receives much more illumination than does the bottom at the depth where oysters are normally found. For several hours a day it is covered by a layer of water only 100 cm thick.

Water temperatures differ very little from that in the bulk of the water in the basin of the Oosterschelde. Perhaps during very hot spells the tidal basin warms up a little more quickly at low tide. But the

incoming tide restores normal temperature conditions a few hours later. The same holds good for salinity, pH, and oxygen-content. Fairly strong currents prevail many hours a day. From a few hours before until a few hours past low tide the basin is filled with slack water.

Life is amazingly abundant in this basin, both in the number of species and individuals. I shall not attempt to enumerate the organisms which can be encountered, but I cannot resist pointing out some of the more conspicuous. Algae are abundant on the dikes, in the sluice-gate, on trays, stones, and shells. Numerous species of Rhodophyceae, Chlorophyceae, and Phaeophyceae have been collected there. *Fucus vesiculosus* L. and *Ascophyllum nodosum* (L.) predominate quantitatively. I want to make special mention of *Ulva lactuca* LE JOL and *Codium fragile* (SUR.) HARIOT, as these species sometimes give cause for anxiety, threatening to smother trays and other apparatus and instruments in the basin. Several fishes have been observed in the small plot of water, of which *Clupea harengus* L., *Clupea sprattus* L., *Pleuronectes flesus* L., *Syngnathus acus* L., *Anguilla anguilla* (L.), *Cottus scorpius* L., *Zoarces viviparus* (L.), *Gobius microps* KRØYER, *Engraulis encrasicolus* (L.), and *Scomber scombrus* L., are the most frequent inhabitants or visitors. The common shore crab, *Carcinides maenas* (L.), is very abundant, and so is *Porcellana longicornis* (L.). The interesting *Macropodia rostrata* (L.) has been encountered several times (e.g. 9-11-1941, 3-9-1940, and recently, 9-9-1949, in great numbers about 800 metres north of this station). *Crangon crangon* (L.) and *Palaemon elegans* RATHKE are abundant, but I also found the green coloured *Thorulus cranchii* (LEACH), hidden between some tile-collectors (e.g. 27-8-1940, 9-10-1941, 17-9-1940). Of the smaller Crustaceans I mention the abundance of *Praunus flexuosus* (O. F. MÜLL.) and *Gammarus locusta* (L.), and the occurrence of *Hyppolyte varians* LEACH, *Melita palmata* (MONT.), *Hyale nilsonii* (RATHKE), *Erichthonius difformis* (M. EDW.) and *Jaera albifrons* LEACH. The Cumacean *Bodotria scorpioides* (MONTAGU) is very abundant between the shell fragments of the superficial bottom layers. The Pycnogonids *Nymphon grossipis* F. (8-9-1942), and *Pycnogonum femoratum* (RATHKE) (4-12-1939) have been collected here. Mussels (*Mytilus edulis* L.) abound, especially attached to the stones of the dikes, and so does *Littorina littorea* L.. A fair number of oysters settle down in this spot, and *Littorina obtusata littoralis* L. lives among the sea-weed. Young individuals of *Mysella bidentata* (MONT.), *Tapes pullastra* (MONT.) and *Mya arenaria* L. and all sizes of *Cardium edule* L. are encountered in samples of bottom material, and so are many *Hydrobia ulvae* (PENN.). The large green Polychaete worm *Nereis virens* SARS can be dug out of the soil and so can *Arenicola marina* (L.), *Nereis diversicolor* O. F. MÜLL., *Capitella capitata* (FABR.) *Scoloplos armiger* (O. F. MÜLL.),

Heteromastus filiformis (CLAP.), and *Nephtys Hombergii* AUD. & M. EDW.

Under shells and pieces of tiles we find the polychaete worms *Lepidonotus squamatus* (L.), *Harmothoe imbricata* (L.), *Harmothoe impar* (JOHNST.) and *Platynereis dumerilii* AUD. & M. EDW., *Lanice conchilega* (PALL.), and *Amphitrite Johnstonei* MALMGREN apparently feel at home here, and the worms *Phyllodoce maculata* (L.), *Eulalia sanguinea* (OERSTED), and *Peloscolex benedeni* (UDEKEM) are found in samples of bottom-material. The sea-anemone *Sagartia anguicoma* PRICE is abundant here, while *Diadumene cincta* STEPHENSON settles on *Ulva lactuca* and other supports. The early developmental phases of the jelly-fish *Aurelia aurita* L. are sometimes very abundant here. The Ascidians *Ascidiaella aspersa* O. F. MÜLL., *Molgula tubifera* (OERSTED), and *Botryllus schlosseri* (MONT.) occur in smaller or greater numbers. The sponge *Halichondria panicea* (PALL.) covers the walls of the sluice-gate and so does the beautiful sponge *Sycon ciliatum* (FABR.), which may also settle on the trays in fair numbers. *Haliclone limbata* (MONT.) weaves a thin and light sponge coating on shells and tiles, and hibernates as gemmulae, which is most unusual for a marine sponge. The Bryozoan *Bugula plumosa* PALL. hangs from walls and trays, while *Lepralia pallasiana* (MOLL) often develops large colonies on stones and shells. The Hydroids *Laomedea gelatinosa* (PALL.) and *Laomedea loveni* ALLM. as well as *Tubularia larynx* ELL. & SOL. have been found here.

I feel sure, that a more thorough survey will reveal the presence of more species still, especially a host of smaller creatures, like Ostracods, Harpacticid Copepods, Foraminifera and other Protozoans.

The species mentioned are enough to show that the station Yerseke, "Kijk-uit" is by no means a biological desert, but that many species, belonging to several phyla, find here a congenial home.

ANNOTATED LIST OF SPECIES FOUND ON SHELLS OF LIVING OYSTERS WITH SOME NOTES ON POLYCHAETE WORMS OCCURRING IN OTHER HABITATS

PHYLUM PROTOZOA

There is not the slightest doubt that a great number of Protozoans should be reckoned among the epifauna of the shells of living oysters. As has been mentioned above, my methods of investigation of this particular habitat did not enable me to observe, collect, and identify species of microscopic dimensions. A binocular lens magnifying $\times 10$ has been used in examining the samples of oysters collected at frequent intervals. Incidental microscopical observations revealed the presence

of a great number of minute organisms on the oyster shell's exterior, but those have deliberately been left out of this list of species.

Still, a few Protozoans figure here because they are of such a large size that they can be distinguished by the naked eye. Some of them may be found so frequently and in such great numbers, that they should be reckoned among the regular denizens of the habitat under consideration.

FORAMINIFERA

Archimonothalamia:

Crithionina heinckei RHUMBLER (fig. 1).

Of frequent occurrence on the shells of oysters is a peculiar organism belonging to the Archimonothalamic Foraminifera. Its exterior appearance is that of a little white dome, usually measuring from 600 μ to 900 μ in diameter. Though the base, attached to the oyster's shell, usually approaches the circular shape, some of them are more elongated or possess one or more rather irregular protrusions. Their colour, snowy or creamy white, renders them conspicuous, even to the naked eye, especially when they are attached to the brown scales of the prismatic layer on the oyster's flat valve. Often an accumulation of some "dirt" of a yellow or greenish brown colour can be observed on one particular spot of the white dome shaped case, sometimes in the centre, sometimes close to the margin. If we brush this dirt away carefully, a tiny hole, from 70 to 110 μ in diameter, is revealed. If we watch carefully and patiently, the animal inhabiting the little white dome may be observed to come out of the tiny hole: a viscous foamy protoplasmic body protrudes, of irregular shape and speckled all over with minute brown spots. Occasionally a narrow or broader stream of protoplasm may creep out of the dome over quite a distance. The protoplasm is able to send out pseudopods, which may be rather broad or of a hairlike shape, which pseudopods may proceed to anastomose. One can observe foreign bodies, among which smaller living beings, becoming included in the flowing protoplasm. The protoplasm does not necessarily leave the dome through the ostium. Some domes do not possess this round aperture. In this case the protoplasmic stream may leave the dome from underneath, flowing out in between the substratum and the dome itself. I presume that the "dirt" usually found on or near the ostium has some relation to the animal's feeding behaviour; a few hours after having been taken away it reappears. It may be interesting to note, that I often encountered small green algae (20 μ), possessing a conspicuous red pigment spot, on the little white dome of *Crithionina*. I cannot say whether or not symbiosis is involved, but it is certainly remarkable

that the wandering protoplasmic stream does not seem to destroy these algae readily.

On the underside the dome is not closed with white material. Therefore it is fairly easy to take the occupant out of it alive. The naked

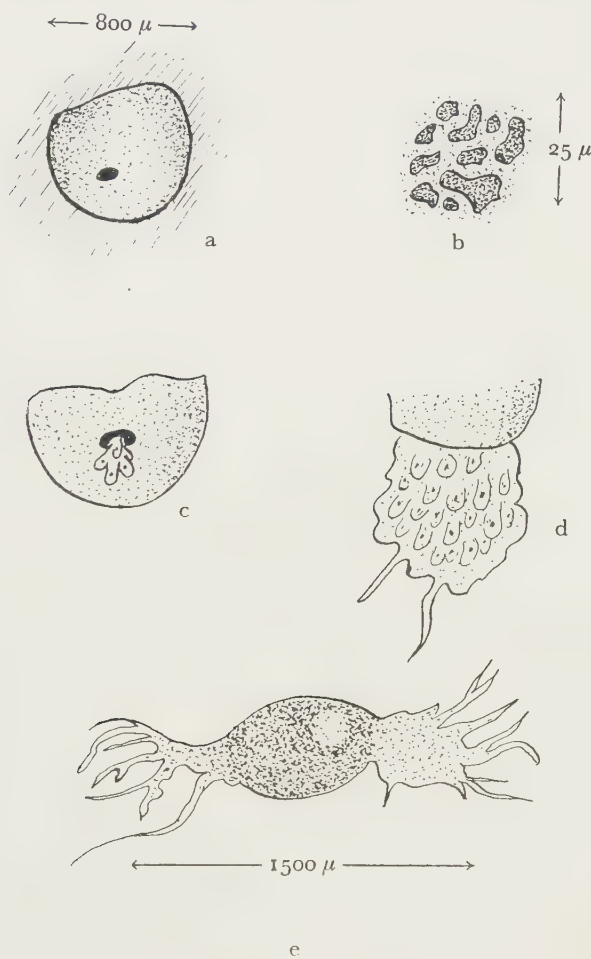


Fig. 1. *Crithionina heinckeii* RHUMBLER; a: case on substratum; b: part of the shell; sand-grains imbedded in organic material; c: animal protruding from its case; d: advanced stage of protrusion; e: case removed, formation of pseudopods.

animal, showing a fairly large round hyaline vacuole in its centre, goes on creeping on its new substratum, making irregular protrusions and pseudopods, some of which may give the animal a hairy or ciliated appearance. Without taking these pseudopods, up to 400 μ long, into consideration, the extended animal may measure up to 1500 μ.

I repeatedly observed that this organism may shift with its dome-shaped case on its substratum. Also that living specimens attached to a tiny piece of substratum only, are able to turn over on the other side if placed in a glass container with sea-water. The latter observation showed me that the little white domes could not be the eggs of any animal, and eventually brought me on the right track to identify this organism as *Crithionina heinckeï*, described by RHUMBLER in 1928.

The little white dome is not stiff but somewhat flexible and is not calcareous, as immersion in dilute hydrochloric acid shows. It has a leathery appearance and is fairly thickly walled (40 to 50 μ). The white dome is moderately smooth and not at all transparent. Observations in incident light show that foreign bodies of irregular shape and size, up to 25 μ long, are imbedded in the dome. The incrustations, which are of a light gray colour, are imbedded mosaic-wise in a very white organic material. Only the incrustations, 5 to 25 μ long, and apparently consisting of silica, remain after igniting.

I did not count the exact number of *Crithionina* on my oysters, but noted down their relative frequency in my quantitative samples as: "absent", "present", "moderate numbers", "fairly abundant", and "abundant". It may be seen from the tables that *Crithionina*, though so far as I am aware thus far only found by RHUMBLER at Heligoland, is far from rare in the Oosterschelde. As a rule, the young oysters recently taken from the tile collectors, with which I started my annual series of sampling, did not bear any *Crithionina* at all. Usually 3 to 4 weeks elapsed before the first white domes were found. From that moment their number was found to increase fairly rapidly to "moderate" or "fairly abundant". They did not disappear when the water temperature dropped later in the year.

Crithionina heinckeï RHUMBLER has not only been observed on shells of oysters in the station "Kijk-uit" Yerseke, as set out in the tables, but also repeatedly on oysters taken from several plots on the Yerseke Bank, Oosterschelde. I also found them on limed tile-collectors West of Yerseke, and attached to *Ulva* and other sea-weeds, e. g. on plot 443 at the South-Eastern tip of the Isle of Tholen, and in the oyster basin made from the ancient Bergen op Zoom water redoubt.

Rotaliaridia:

Rotalia beccarii (L.)

A fairly large polythalamous Foraminiferan has been collected on the shells of the oysters kept in the station "Kijk-uit", Yerseke. Miss W. VAN DE GEYN kindly identified it as *Rotalia beccarii* (L.). This species appeared to be extremely abundant in the superficial bottom layers of the oyster basin in which I kept my experimental trays. I therefore

consider its presence on my oysters, where it has usually been found among the sandgrains and detritus particles in the crevices of the shell, as purely accidental.

On several other occasions I found this Foraminiferan on the shells of oysters taken from the regular plots of the oyster farmers. As this *Rotalia* can be found in great numbers in many places in the Oosterschelde, and elsewhere along the Dutch coast, the occurrence of a few on the shells of oysters can hardly be avoided.

CILIATA

Heterotrichida:

Folliculina ampulla MÜLLER (fig. 2).

A third Protozoan of fair dimensions, and this time of a conspicuous coloration as well, belongs to the epifauna of oysters. This creature, living in a well-shaped bottle green case, can be found in this habitat so regularly and in such great numbers, that it should be reckoned as a characteristic inhabitant. Thousands of tiny little ampullae may be found to cover the oyster shells. It is one of the first creatures which settles inside the empty shells of recently died oysters. Its green colour renders it very conspicuous, even to the naked eye, against the glossy white shells.

This Protozoan, usually measuring from 200 to 800 μ , was tentatively identified as *Folliculina ampulla* MÜLLER. REES (1883) has already noted this species in his list of Protozoans found in the Oosterschelde, but he only came across occasional individuals and did not find the dense populations on the shells of oysters or inside empty shells. I believe that *Folliculina ampulla* is a fairly important member of the epifauna of the oyster. Under natural conditions, two slender peristomal lobes protrude from the free end of its case in search for food, which is undoubtedly taken out of the surrounding sea-water. Judging from its rapid increase in numbers inside empty shells and on the shells of my experimental oysters, its growth and reproduction must be rapid at least in the summer season. Therefore, *Folliculina* may be important as basic food for many members of the oyster's epifauna. In fact I witnessed the Foraminiferan *Crithionina* ingesting a *Folliculina*. I cannot support SCHODDUYN's view (1927) that *Folliculina* clears away dead bodies of oysters. In this crabs and similar marauders, as well as micro-organisms, which are soon counted by the billions, will be far more effective. May be SCHODDUYN misinterpreted *Folliculina*'s rapid settlement of the interior of empty shells of recently died oysters.

I noted the occurrence of *Folliculina* in my tables in the same way as has been done for *Crithionina*, making a rough estimation of their abun-

dance. From my data it can be deduced that *Folliculina* increases in number in the course of the season, and does not disappear readily when water temperatures start to drop later in the year. In fact I repeatedly observed specimens feeding actively in mid-winter.

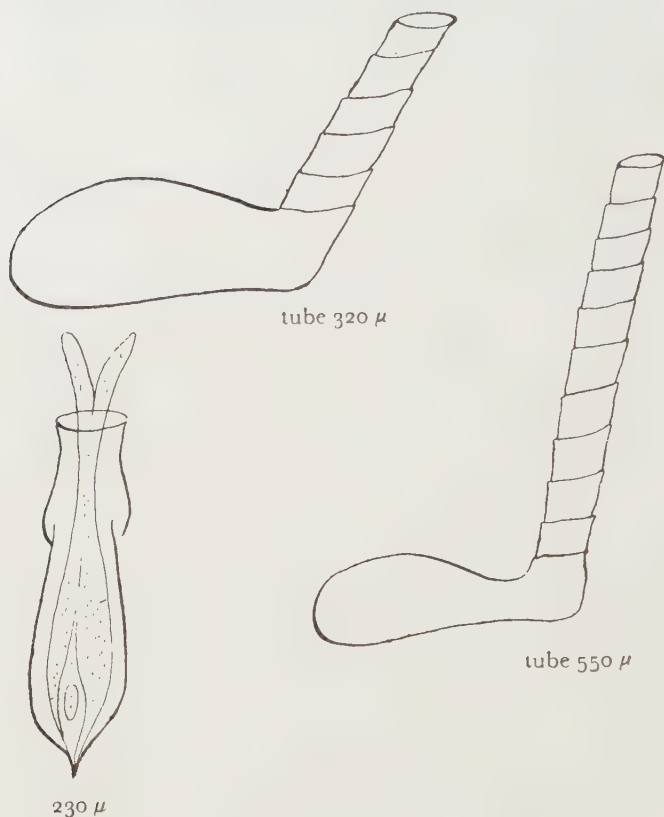


Fig. 2. *Folliculina*'s from an oyster shell, Oosterschelde

The lesser fluctuations in its occurrence set out in the tables may be due partly to the fact that I did not make exact counts of the numbers of *Folliculina*, and partly to a certain equilibrium between its reproduction and the losses suffered regularly.

After reading Das' 1949 paper, I became aware that a creature named *Folliculina ampulla* MÜLLER may not exist at all, but that the specimens observed might belong to another, perhaps even to several different species. Many authors identified tentatively the *Folliculina* encountered as *Folliculina ampulla* MÜLLER, and overlooked the differential features. DAS states: "There is no gainsaying the fact that

many different species of *Folliculina* have been recorded as *Folliculina ampulla* by past workers. I have strong suspicion that the species *Folliculina ampulla* is really non existent." I found that this holds good for the species living in the Oosterschelde, and recognized later: *a.* the large species *Folliculinopsis producta* (WRIGHT) with its multiple nucleus, and its long tubes placed vertically on the ampullae, which shows 10 to 12 spiral thickenings; *b.* *Folliculinopsis andrewsi* (HEDŽI), which is somewhat smaller, has a wider ampulla and only 5 to 8 spiral turns on the tubes, which are often placed obliquely; *c.* and a smaller species still, with a single nucleus and an ampulla of about 230 μ long with a typical constriction at its free end. The case of the latter species stands upright on its tip. Most probably it is a species of *Parafolliculina*, perhaps *P. hirundo* (KENT), though this species should have a smaller case and a paler colour, and moreover is said to live horizontally.

Since it is perfectly impossible to find out afterwards which species of *Folliculina* predominated on the shells of my experimental oysters in the years 1941-1945, they will figure together in the tables as *Folliculina ampulla*.

I have seen them in great numbers not only on living oysters and in empty shells on many oyster plots, but also on the lime-coating of tile collectors, and on mussel shells used as collectors.

PHYLUM PORIFERA

CALCAREA

Sycon ciliatum (FABR.)

This rather small, approximately cylindrical sponge of creamy white colour, with a large and fringed single osculum at its free end, is far from rare in the Oosterschelde. It can be found hanging, osculum downward, on tile collectors and on the vertical parts of the walls of tidal basins at Yerseke. Many years ago, the late Prof. VOSMAER, a Dutch sponge specialist, found this species in great numbers on the tile collectors of the Yerseke oystermen. In certain years *Sycon ciliatum* appeared to settle on my experimental oysters at Yerseke too. I consider its occurrence there as accidental, and do not reckon this sponge among the creatures living by preference in this habitat. The frequency of its occurrence on my oysters can be judged from the tables. It is my impression that this sponge flourishes especially in the months of August and September.

Leucosolenia botryoides (ELL. & SOL.).

For the sake of completeness I mention this delicate little sponge, re-

sembling a richly branched dead discoloured piece of red-weed. I found it occasionally in September and October in my oyster-trays in the station "Kijk-uit", Yerseke, e.g. 19-10-1943. It seems to be rather rare in the Oosterschelde.

MONAXONIDA

Clione celata GRANT.

Oystermen from many different countries are familiar with the boring sponge, and the ravages it can bring about among their oysters. Oyster fishers knew this pest long before GRANT described it from the Scottish oyster beds. The members of the family of the Clionidae excavate galleries in the shells of molluscs and in other calcareous material. A literature far too extensive to review here deals with the boring sponges and with their relations and influences on oysters and the oyster industry. Locally (e.g. in North Carolina, South Carolina, and Georgia, U.S.A.) their influence is so great that oyster farming below low water level seems impossible, at least in waters of rather high salinity. Though more than a dozen species of *Clione* are said to inhabit oyster shells, only *Clione celata* GRANT has been found in the Dutch waters.

Though serious damage has been recorded from the French Atlantic coast, where according to GIARD (1881) entire oyster beds have been destroyed by the boring sponge, the Dutch oystermen did not complain about it until the year 1886. HOEK (1887, 1902) remembered having encountered only occasional individuals on the Dutch oyster beds during the 1883-1884 investigations. The boring sponge increased so much afterwards, that the fisheries report for 1886 makes a special note of it. In his 1902 report on the difficulties met with in the Dutch oyster industry, HOEK counted up to 10% of the oysters affected by boring sponge on his experimental plot. HOEK also mentions having found high percentages of oysters affected on a natural oyster bed near the Isle of Terschelling in the year 1899.

Nowadays the boring sponge is hardly noticed on the Dutch oyster beds. Occasionally one comes across an oyster with honeycombed shells from which the sponge's slightly retractable sulphur-yellow "heads" protrude. One may investigate hundreds of Dutch oysters, grown under low water level, without coming across a shell attacked by *Clione celata*. The older the oyster, the greater the chance that it eventually becomes infected with *Clione*. Therefore the boring sponge is rather frequently found in old oysters attached to stones at the foot of the sea dikes in the Zealand waters. Its occurrence in oysters one or two years old is very rare indeed. I never found it in my experimental oysters. Therefore *Clione celata* does not appear in my tables.

This is not the place to give a treatise on *Clione* and its influence on the oyster industry. I want to make a few remarks, however, on its frequency of occurrence and on its relation to the oyster. No doubt the records of detrimental influence by the boring sponge found in the Reports of the Fishery Board of the Zealand Streams coincide with periods of neglect and overpopulation of the beds, during which the oysters showed a slow growth only, and many beds were overrun by "weeds" and "pests". I ascribe the very limited incidence of boring sponge nowadays at least partly to a regular and thorough cleaning of the oyster beds, and rapid growth of the oysters. The Dutch oystermen do not apply any special methods of control against the boring sponge, such as relaying the oyster on beds exposed at low tide, as was advocated by TOPSENT (1900), or bathing the oysters in fresh water to kill *Clione*. Should *Clione* ever come to affect a greater number of our oysters, I feel sure that our oystermen, who clean their beds at least once every two years very carefully, and sort their oysters ashore, would dip all their oysters in a disinfectant before relaying them, as is done now against *Crepidula* and shell disease.

Clione celata is not a true parasite of the oyster. It excavates its galleries in the shells of oysters only to create an adequate habitat. Here again living oysters ensure better protection against silting than empty shells. Several investigators (e.g. HOEK, 1902) recognized that a light or moderate attack of *Clione* does not do appreciable damage to the oyster. The edible parts of the oyster may remain in perfect condition notwithstanding the presence of *Clione*. The affected oyster's shell, however, becomes brittle, and may easily break during packing and transportation. No Dutch oysterman would think of packing an oyster seriously affected by *Clione*. The evil smell of a broken *Clione*-infected shell might spoil his pack.

Both HOEK (1902) and TOPSENT (1900) claim that a heavy attack may cause appreciable damage to the living oyster. TOPSENT observed that the oyster struggles against *Clione* by depositing little patches of conchyoline at each menaced point. I can corroborate this observation. Wherever *Clione* threatens to perforate the oyster shell, the oyster responds by sealing it off with a patch of greenish-yellow conchyolin. In exactly the same way it acts against shell perforations caused by *Polydora ciliata*. It seems probable that the oyster begins to suffer when owing to the enhanced activity of *Clione* the sealing off has to be repeated on a large scale and with great frequency. As soon as the oyster fails to keep the *Clione* well covered by conchyolin, it breaks down. The first sign is a discolouration of the oyster's mantle tissue opposite the sites where *Clione* is on the point of perforating the shell. Next, the entire oyster becomes discoloured, weak and often thin; then

death is approaching. It can be seen that the shells of recently died oysters are just or hardly perforated by *Clione*. Probably *Clione*'s excretions (the same which are involved in the still rather mysterious work of boring the galleries?) strongly affect the living tissues of the oyster. MEDCOF (1949) demonstrated that similar relations exist between *Clione* and scallops.

Apart from its being an oyster pest, the Dutch oystermen hate the boring sponge because of its disagreeable odour, resembling that of crude phosphorus, and especially because its specules often bring about nasty and inconvenient infections in the hands of those engaged in the sorting and grading of oysters.

CORNACUSPONGIDA

Halichondria panicea (Pallas) FLEM.

The crumb-of-bread sponge is very common in the Oosterschelde. Even in the tidal basin at Yerseke used in the work discussed in this paper, it occurs in numbers. Occasionally it settles on an oyster or on an empty oyster shell, and in time often envelops them completely. Though the losses thus effected on the Dutch beds are hardly worth mentioning, it may be different elsewhere. Thus MOEBIUS (1893) informs us that many oysters were severely smothered and ultimately killed by *Halichondria panicea* on the natural oysters bed investigated by him.

Halichondria panicea did settle on my trays but not on my experimental oysters, and therefore does not figure in the tables.

Haliclone limbata (MONT.).

Often some of my oysters kept on trays at Yerseke became partly or entirely covered with a light spongy growth of a yellowish gray colour. Only rarely did the spongy material develop the shape characteristic of a sponge, complete with oscula. Under the thin layer of spongy material I often found extensive fields of yellow pellets, one layer thick, as if some moth had deposited her eggs on the oyster shell. I assumed that the pellets were the gemmulae of the sponge, though I did not know of any marine sponge hibernating as gemmulae. Dr VERVOORT of the Leyden Museum of Natural History finally managed to identify this sponge as *Haliclone limbata* (MONT.). It is interesting to note that VOSMAER too (1882) collected this peculiar sponge only near Yerseke. Though VOSMAER then named it *Chalinula fertilis* (KELL.), preserved material collected there by him in August 1887 was used by VERVOORT to demonstrate that it is identical with the species *Haliclone limbata* (MONT.), described in detail by several other authors (e.g. GRENTZENBERG, ARNDT, TOPSENT).

Haliclone appeared year after year on my experimental oysters at Yerseke, though it is met with only occasionally in other places in the Oosterschelde. The tidal basin used by me seemed to be especially attractive to *Haliclone* since not only oysters, but also old tile collectors, shells, etc., were liable to become covered by this sponge. I noted in the tables whether or not *Haliclone limbata* occurred in my samples and tried to estimate its abundance. Further I made a note on the appearance of gemmulae. The yellow gemmulae are not of a very regular shape, though approximately of the same size. According to Dr VERVOORT the gemmulae contain smooth speculae and a porus, sometimes two. No doubt the sponge hibernates as gemmulae. Early in summer only gemmulae can be detected, at least on oysters which sojourned in the tidal basin at Yerseke the year before. In mid-summer the sponge cover develops from the gemmulae. As a rule it remains thin and rather shapeless. Sometimes it grows higher and develops real oscula. In mid-summer its colour is yellowish gray, sometimes mixed with a red tinge. Later (August) grey clouds rise from the sponge whenever touched (reproduction?), and in the autumn grey is the general colour. The sponge disappears in early winter. That the formation of gemmulae is not delayed till the water temperature drops steeply, can be seen from the tables. Often gemmulae are abundant as early as August, or in September when rather high temperatures prevail still.

It is interesting to note that this sponge was not present on the young oysters with which I started my experiments in early summer, but settled on their shells in the course of the summer season. Its presence was usually apparent in July. Formation of gemmulae started later in August or in September. Oysters one year older and already infected with *Haliclone* the year before probably had living gemmulae on their shells at the time I started my epifauna-observations. Hence the finding of *Haliclone* as early as June on these oysters. Nevertheless the formation of a new generation of gemmulae started at about the same time as on the oysters one year younger.

The gemmulae apparently are quite hardy, since this sponge was normally abundant after the unusually severe winters 1939-'40, 1940-'41 and 1941-'42. Though they were not exposed to low air temperatures, they had to endure water temperatures of -1.7° C for many weeks in succession. The same holds good for the majority of the other species mentioned in this study.

PHYLUM COELENTERATA

HYDROZOA

Though the saline waters of the Oosterschelde are favourable to many hydroids, which can be found living attached to sea-weeds, stones, buoys, sea-marks, and similar supports, representatives of this group occurred only occasionally on my experimental oysters.

Tubularia larynx ELL. & SOL.

This well-known hydroid often grows abundantly on the trays in which the oystermen rear their young oysters, about a mile N. E. of Yerseke. I only found a few colonies on my trays in the tidal basin of the station "Kijk-uit", Yerseke, and rarely one on my oysters.

Laomedea loveni ALLMANN, and *Laomedea gelatinosa* (PALLAS).

These species, often occurring in abundance in the Oosterschelde, have been collected occasionally on my experimental oysters. Their share in the biocoenosis found at Yerseke on the shells of living oysters appeared to be very modest, indeed. The hydroids mentioned in the tables all belong to the genus *Laomedea*. Though samples of oysters collected in other stations in the Oosterschelde were poor in hydroids too, this will not necessarily hold good for oyster beds in other countries.

SCYPHOZOA

Aurelia aurita L.

A very interesting member of the epifauna of my oysters at Yerseke was the scyphistoma of the jelly-fish *Aurelia aurita*. Year after year this jelly-fish makes its appearance in the waters of the Oosterschelde in early summer. During May and June especially it may be seen in countless numbers, its four horseshoe-shaped gonads then full of spawn. Some fishermen claim that this jelly-fish migrates inshore in the spring, and that they start to catch them in their shrimp trawls long before we can admire their graceful appearance in the surface waters of the Oosterschelde. HOEK's observation (1884), made during his collecting cruise from 11-16 April 1882, that enormous numbers of *Aurelia* then occurred in the deeper layers of the Western part of the Oosterschelde, may confirm this view. Recent observations (VEWERY, in litt.) adduced evidence, however, that *Aurelia aurita* is a purely inshore species. Particularly enough, we do not know very much about *Aurelia*'s life cycle in Dutch inshore waters. The adults are abundant in early summer, and gradually disappear later. There are reasons for assuming that the adult jelly-fishes met with in summer are only a few months old, and

that the growth rate from ephyrae to adults must be amazingly rapid. Though we should expect an abundance of scyphistoma on submerged objects in Dutch inshore waters, they have rarely been found there. It was a pleasant surprise to find a great number of scyphistoma of *Aurelia aurita* on my experimental oysters at Yerseke in the summer of 1941. They apparently did quite well in that station, and reappeared year after year, though only in some years in great numbers. The graceful polyps settled on my oysters and on the trays, and also on old lime-coated tile collectors, and similar objects. Some years I also found them in the oyster basin constructed in the old water redoubt of Bergen op Zoom. On the other hand, samples of oysters taken in other stations never bore these scyphistoma.

The polyps settled late in June or early in July, which is in accordance with the abundance of mature jelly-fishes in the month of June. Their number may increase in the course of the summer, but the growth shoots of the oysters put on later in the season were initially free of them, indicating that no more scyphistoma settled down. As the polyps are able to move about on the substratum as can easily be observed in the laboratory, they are inclined to spread more evenly over the oyster shells in the course of time. Oysters brought into the station Yerseke, "Kijk-uit" later in the season (e.g. August 23rd, 1943), remained free of *Aurelia* polyps, indicating that no more polyps settled from the plankton as late as that. Peculiarly enough, the last sample taken of these oysters (6-10-1943) contained a few scyphostoma. Probably they migrated to the oysters from the wire netting of the trays. The latter had been in Yerseke since month of May.

Another interesting point is that my data set out in the tables provide no indication that the scyphistoma hindered or scared other members of the habitat. Though many scyphistoma occurred on the oysters 2 years old in August and September 1941, in September 1942 and from July 14th to August 23rd, 1943, there is no evidence that this had any appreciable influence on the frequency of other creatures living on the shells of the oysters concerned. For this the non-sedentary Polychaet worms, usually occurring in great numbers, are especially good indicators.

It can be seen from the tables that the first scyphistoma were observed on June 30th in 1941, on June 30th in 1942, June 29th in 1943, July 13th in 1944 and July 3rd in 1945.

Strobilation has been observed too, especially in the year 1943, when this process started as early as August 30th. In October and November of that year most of the polyps were divided into discs and the first ephyrae detached themselves. This has been described and depicted in detail by Prof. BURGERS (1944), an amateur biologist, whom

I provided with material from the station "Kijk-uit", Yerseke. VERWEY (1942, 1949) assumes that strobilation as early as October and November is abnormal, and that the ephyrae produced so early will have little or no chance of survival. According to him the bulk of the jelly-fishes found in early summer will have started off as ephyrae in early spring.

We eagerly wait for further information and still wonder where the incredible number of *Aurelia* observed in early summer originate. Do their scyphistoma live on stones at the foot of our sea-dikes, or on supports further offshore? Surely the few from my station at Yerseke cannot provide them all.

ANTHOZOA

Sagartia anguicomma PRICE (s. *S. viduata* GOSSE).

Occasionally a few specimens of this sea-anemone appeared to have settled on my experimental oysters. Since this anemone is most abundant in the tidal basin in which my trays were placed, its occurrence on oyster shells is no surprise. I wonder, however, how the anemones reached my oysters. It can hardly be assumed that they managed to crawl into the trays, climbing the concrete supports, and thus reaching the oysters 25 cm above the bottom. On the other hand, the individuals encountered were of a fairly large size. Therefore I do not believe that they were very young individuals recently settled down from the plankton. Perhaps rough weather and wave action hide the secret of their migration.

Sagartia anguicomma is fairly regularly found on oysters in other stations, especially where the subsoil consists of a mixture of sand and mud rich in shell fragments. Since those oysters are in immediate contact with the bottom, it is easily understood how *Sagartia* can reach them.

Diadumene cincta (STEPHENSON).

This little brick-red sea-anemone is frequently met with in the station "Kijk-uit", Yerseke. It is especially conspicuous when it settles down on the green leaves of *Ulva lactuca*, but lives on other substrata too. Thus it has been found occasionally on my experimental oysters in this station. I do not claim that this and other sea-anemones select oysters as an exceptionally favourite habitat.

PHYLUM PLATHELMINTHES

TURBELLARIA

Plagiostomum vittatum LEUCKART.

This slender spindle-shaped Rhabdocoelic Turbellarian worm, bearing three conspicuous bands of purple pigmentation transversely, has been observed a few times, crawling about actively on the oyster shells. I found it at Yerseke (2 specimens) on June 16th, 1941 and again (1 specimen) on June 16th, 1942. Later, I collected 3 specimens among oysters living on trays in the basin at Bergen op Zoom (August 5th, 1942). I have never come across it since. Apparently it is a rare visitor on the shells of living oysters.

NEMERTINI

Lineus ruber L.

Under stones and shells, and in mud collected between tile-collectors *Lineus ruber* is frequently met with. It a slender worm with a spatulate head, showing fairly deep head splits. It tapers posteriorly and is capable of impressive contractions and expansions. It has a dark bottle green colour. Some individuals, however, have a red-brown tinge. Occasionally I found it on my oysters, hidden in the mud deposits between the scales of the prismatic layer of the flat valve.

I rarely found *Lineus ruber* on the young oysters, entering their second summer. On oysters one year older (included in my investigations in the years 1941, 1942, 1943) I encountered a fair number of this Nemertean throughout the season. The greater amount of shelter offered and the fair quantities of mud and silt deposited between the scales of the flat valves of those older oysters apparently suited this species. *Lineus ruber* is said to feed on Annelids. Possibly it affected the composition of the Annelid fauna on the shells to some extent. The tables give no indication that this effect has been of a devastating character, however.

Tetrastemma flavidum (EHRBG.).

Another Nemertean worm, most probably *Tetrastemma flavidum*, with its four eyes and its pale pinkish-yellow colour was encountered a few times on my oysters at Yerseke, e.g. 20-5-1942, 14-7-1942, 5-7-1943, 13-9-1943, 22-6-1944. Its influence on the equilibrium of the bio-coenosis of the oyster shells must be a very restricted one.

PHYLUM ASCHELMINTHES

NEMATODA

Nematode worms have often been found crawling about on the shells of the oyster, and especially between the scales of the flat valves. Their number was very modest as a rule (usually less than 1 per 10 oysters), and their influence presumably correspondingly limited. I collected the Nematode worms quantitatively in the years 1941, 1942, and 1943 only. These specimens have been identified by Dr J. H. SCHUURMANS STEKHOFEN. In the years 1944 and 1945 I did no more than make an estimation of their total abundance.

The specimens collected in my 1941 series of samples have been mentioned in SCHUURMANS STEKHOFEN's 1942 paper, in which the author wrongly commented on a possible detrimental effect of the Nematodes, thought to be living in the oyster's mantle cavity. The Nematodes were collected on the exterior surface of the oyster shell, however, and none of them was found in the mantle cavity.

Of the Nematodes found, only *Enoplus communis* BASTIAN and *Oncholaimus skawensis* DITLEVSEN occurred in fair numbers, so that they can be reckoned as part of the regular epifauna of the oyster. The other species are more or less accidental visitors. As I cannot contribute anything new on the biology of the Nematode worms encountered, I shall confine myself to a list of the species found:

- | | |
|--|---|
| 1. <i>Anticoma limalis</i> BASTIAN | 10. <i>Symplocostoma longicolle</i> BASTIAN |
| 2. <i>Thoracostoma figuratum</i> (BASTIAN) | 11. <i>Enchelidium marinum</i> EHRENBURG |
| 3. <i>Thoracostoma trichodes</i> (LEUCKART) | 12. <i>Cyatholaimus demani</i> FILIPJEV |
| 4. <i>Enoplus communis</i> BASTIAN | 13. <i>Praeacanthonchus punctatus</i> (BASTIAN) |
| 5. <i>Enoplus brevis</i> BASTIAN | 14. <i>Euchromodra vulgaris</i> (BASTIAN) |
| 6. <i>Adoncholaimus fuscus</i> BASTIAN | 15. <i>Chromadorita ditlevseni</i> DE MAN |
| 7. <i>Oncholaimus skawensis</i> DITLEVSEN | 16. <i>Monoposthia costata</i> (BASTIAN) |
| 8. <i>Metoncholaimus pristiurus</i> ZUR STRASSEN | 17. <i>Theristus setosus</i> BUETSCHLI |
| 9. <i>Eurystomatina filiforme</i> DE MAN | |

In samples of bottom material taken in the tidal basin in which I worked I found *Enoplus communis* BASTIAN, *Siphonolaimus niger* DE MAN, and *Anticoma limalis* BASTIAN; the latter in great numbers.

Also on oysters collected on the plots of the oystermen I occasionally found some Nematodes. Here too *Enoplus communis* BASTIAN preponderated numerically.

PHYLUM ANNELIDA

POLYCHAETA

Aphroditidae:

Lepidonotus squamatus (L.).

Since MOEBIUS (1893) recorded the finding of many specimens of *Lepidonotus squamatus* on the natural oyster beds he investigated, this worm has been collected in several other oyster districts. HORST (1884) stated earlier that *Lepidonotus* is abundant on the Dutch coast, which he confirmed later (1896). Specimens from many a locality along the Dutch coast have been preserved in the Leyden Museum of Natural History. LELOUP (1940) found it in the Bassin de Chasse at Ostend, where he carried through an oyster culture project.

It is not at all difficult to spot this yellow and sluggish worm in the oyster district of the Oosterschelde. It can be found on tile-collectors, on oysters, and hidden under stones. It is very slow in its reactions, and is easy to catch. Its identification offers no difficulties: its 12 pairs of yellow or light brown scales, fringed laterally, are characteristic enough.

I found it in moderate numbers on my experimental oysters at Yerseke. Both the finding of young specimens and the increase of the number of *Lepidonotus* per oyster demonstrate that it settled from the plankton in mid-summer. In comparing oysters one year old with oysters which had entered their third summer, my data can be arranged as follows:

Year	Oysters born in	Period of increase in numbers and predominance of young specimens	Maximum number
1941	1940	25/6 — 11/8	1 per 5 oysters
1941	1939	25/6 — 17/9	1 per 3 oysters
1942	1941	30/6 — 14/7	1 per 5 oysters
1942	1940	30/6 — 20/7	1 per oyster
1943	1942	5/7	1 per 5 oysters
1943	1941	29/6 — 14/7	1 per 3 oysters
1944	1943	few only	1 per 12 oysters
1945	1944	18/6 — 3/7	1 per 10 oysters

These figures suggest that *Lepidonotus* breeds in mid-summer, though it should be stressed that my data cannot give much information about the events in the period between the months of November and May, during which my oysters wintered in the Basin at Bergen op Zoom.

In my plankton samples used for the predication of the setting of oysters, I repeatedly observed very young but easily recognizable individuals of *Lepidonotus*. I recorded their occurrence e.g. in the samples of the 15th, 17th, and 19th of June 1942, but saw them on other occasions too. Only later (THORSON, 1946) I learned that *Lepidonotus*' larvae have not yet been described properly.

I also found *Lepidonotus* on oyster samples taken from the plots of the oystermen. Only twice: 21-10-1940: p. 417¹, and 4-4-1941: p. 524 in such great numbers, that almost every oyster bore a *Lepidonotus* on its shell. I do not know what kind of food *Lepidonotus* takes nor the nature of its relations to the living oyster.

Harmothoë imbricata (L.).

It is not difficult to distinguish *Harmothoë imbricata* at first sight from *Lepidonotus*. Its 15 pairs of smooth scales, as well as some other characteristics can be used to identify this species. Like *Lepidonotus*, *Harmothoë imbricata* is common on the Dutch coast. Many specimens are present in the Leyden Museum, and HORST (1884) collected it at Wemeldinge. LELOUP (1940) found it at Ostend. *Harmothoë imbricata* is very common in the tidal basin at Yerseke where I placed my trays with oysters. It can be found there under old tile-collectors and under stones. I also saw it repeatedly on tile-collectors near Wemeldinge and near Strijenham (Isle of Tholen).

Peculiarly enough it is but rarely found on oysters. Though it abounded in the tidal basin, only very few individuals have been found on my experimental oysters. The same holds good for other stations. I only found it twice on samples of oysters taken from the oyster plots: p. 417 21-10-1940, and p. 524 4-4-1941. From my observations at Yerseke I feel sure that these low figures are not due to *Harmothoë*'s swimming away during the sampling.

Could it be that this species reproduces in mid-winter or early spring, so that young individuals had no chance of settling on my oysters? Its absence on oysters remaining throughout the year on the plots of the oystermen does not support this suggestion. Moreover THORSON (1946) found its larvae in spring, summer, and autumn, and but rarely in winter. He found young stages frequently in July and August. There is no reason to assume that this species behaves differently in the Oosterschelde.

I therefore conclude that the shell of the living oyster apparently does not suit *Harmothoë imbricata* as a habitat.

¹ p. 417 means: plot 417 in the eastern part of the Oosterschelde, referring in this to the charts published by the „Fishery Board of the Zealand Waters” (Bestuur der Visscherijen op de Zeeuwsche Stroomen).

The specimens collected in the Oosterschelde, measuring from 20 to 33 mm as a rule, show a wide variation in coloration. Some are of a warm speckled and clouded brown, others of a plain glossy light brown shade; the majority, however, has a broad dark-brown, almost black, glossy band along the back, and is of a very light shade laterally.

Harmothoë impar JOHNSTON (fig. 3).

There is good reason to pay special attention to *Harmothoë impar*, as this is one of the most conspicuous members of the epifauna of the oyster. HORST (1884) mentioned its occurrence in the Oosterschelde. FERRO-NIÈRES (1901) found it in oyster parks at Le Croisic, and LELOUP (1940) detected it in the Ostend Bassin de Chasse, under stones, tile-collectors and among his oysters.

HORST (1896) withdrew his identification later, and renamed the species collected in the Oosterschelde *Lagisca propinqua* (MALMGREN). Fortunately his specimens have been preserved in the Leyden Museum of Natural History, so that I could recheck HORST's identification. I find that there is not the slightest doubt that HORST's first identification as *Harmothoë impar* was the correct one. Professor FAUVEL has been so kind as to confirm my view. *Harmothoë impar*, as collected by HORST and by me, has 35 to 40 setigerous segments. Its unpaired median antenna, more than twice as long as the paired antennae, shows a threadlike distal part. The palps are provided with papillae. Antennae and peristomial cirri bear long club-shaped papillae. The 15 pairs of elytrae (scales), which cover practically the entire body, bear a distinct fringe. The upper setae of the notopodia are doubly pointed, the lower ones show a single point only. The segments not provided with elytrae bear distinct dorsal protuberances. The posterior segments show olive-green spots at the bases of the cirri. The individuals collected by me measured 12 to 25 mm, but those of 20 mm and larger were rare. Some specimens differed somewhat in colour from the general pattern: they showed plain orange-brown elytrae, without cloudy markings. Of others the body was slightly purple under the scales, which gave the entire animal a dark appearance.

In the field it is fairly easy to recognize *Harmothoë impar*, and to distinguish it from *Harmothoë imbricata* and *Lepidonotus squamatus*. *Harmothoë impar* seems to be more lively. It is brisk in its movements, even at water temperatures as low as 5° C. It is usually found in folds and crevices of the oyster shells. In older oysters also it occurs in appreciable numbers between the scales of the flat valve. On tile-collectors it lives in tiny holes in the lime coating or close to some protruding object, e.g. a young oyster. If touched, it tries to crawl deeper in its hiding place. If this does not help, it often tries to wriggle away with brisk

movements. Under water, escape by swimming is possible. *Harmothoë impar* does not make the smooth appearance of *Harmothoë imbricata*, because the former curls its dorsal cirri upwards.

Though I did find *Harmothoë impar* in small numbers in some other habitats (e.g. on tile collectors with and without oyster spat; Wemeldinge, Tholen) I consider the shells of living oysters as its favourite abode, at least in the Oosterschelde. Its occurrence on my experimental oysters can be summarized as follows:

Year	Oysters born in	Period of increase in numbers and predominance of juvenile specimens	Maximum number
1941	1940	4/7—31/7, and in September	1 per oyster
1941	1939	16/6—4/7; 18/8	2 per oyster
1942	1941	30/6—20/7; 25/8—15/9	3 per oyster
1942	1940	9/6—16/6; 30/6—20/7	3 to 4 per oyster
1943	1942	8/6—20/7; 23/8—October	1 per oyster
1943	1941	8/6—14/7; 30/8—6/10	3 to 4 per oyster
1944	1943	22/6—23/8	1 per 2 oysters
1945	1944	5/6—3/9	1 per oyster

From this it can be concluded that *Harmothoë impar* breeds in summer, and that young individuals settle down in June and July, sometimes again in September. In some years the intensity of its setting shows marked peaks, in other years its setting appeared to be a rather protracted phenomenon. Here again, it should be mentioned that my observations cannot prove that *Harmothoë* did not breed at all in winter and early spring. Very young individuals of *Harmothoë impar* have been observed by me in plankton samples. Both its morphological features and its characteristic behaviour (I always examined living plankton) banished all doubt about its identity. I did not record systematically the number of Polychaete larvae found in plankton samples. As my time was often too limited in summer, I could not always examine the plankton samples myself. In several years I found *Harmothoë impar* in the plankton in the last ten days of June and early in July, which tallies with the observations on juvenile specimens, tabulated above. I never investigated plankton samples in September, the spatfall of the oysters being over then.

Harmothoë impar, being so conspicuous and numerous on oysters (I usually found from 1 to 3 individuals per oyster) I wondered what could be its relations to the living oyster and to the other members of the oyster's epifauna. Some experiments were carried out in the lab-



Fig. 3. *Harmothoe impar* JOHNSTON; a. head, dorsal view; b. elytrum; c. notoseta; d. neuroseta; e. parapodium

oratory to investigate *Harmothoe impar*'s way of living. To find out whether or not living oysters attract adult specimens of *Harmothoe impar*, I placed a fair number of them in shallow trays with sea-water the bottom of which was covered with fine sand, and some oysters. Some of the oysters were living, others just empty shells glued together. 24

hours later I counted the number of *Harmothoë* on the oysters, then chased the worms away and left them in peace for a second period of 24 hours. *Harmothoë* apparently disliked the sand and most of them settled on the oysters. Contrary to expectations, the dummy oysters appeared to be nearly as attractive as the living oysters. I repeated this experiment many times and found only rarely a preference for the living oysters, worth mentioning. It appeared to be irrelevant whether the cupped or the flat valve of the oysters had been uppermost. If given a free choice between oysters, pebbles, and different small shells, placed on a sandy bottom, *Harmothoë* left the sand and settled on each of the types of objects offered. Oysters, and shells offering a good shelter (e.g. the deep umbo of *Cardium* shells) were preferred to *Mytilus* shells and smooth pebbles. Shelter probably is the most important factor.

Another point was, whether or not *Harmothoë* is sensitive to light. I covered the trays with sea-water with a sheet of glass, partly blackened, and observed the *Harmothoë* after having been left in peace for 24 hours. Next I turned the glass 180° so that the light and dark parts of the dish were interchanged. *Harmothoë* always showed a marked preference for the dark part of the tray. It apparently prefers a shady place.

To investigate whether the living tissues of the oyster attract *Harmothoë impar*, I placed the worms in a shallow tray with oysters, of some of which I had exposed part of the mantle by taking away a piece of the shell. Though I occasionally saw a *Harmothoë* poking inquisitively with its extensible palps at the bare piece of the mantle tissue, there was never a general rush for the defenseless mollusc. I often kept my *Harmothoë* for days without food before making the experiment. *Harmothoë* was more active at night (though some did not move from one spot in 24 hours), but by next morning the shell of the wounded oyster hardly had more *Harmothoë* than those of the other oysters. I never saw any wounds or damage to the bare piece of the oyster's mantle tissues. Still, on living oysters, *Harmothoë* usually settles down in the shallow furrows of the cupped valve, its head towards the shell's margin. It sometimes seems to touch the oyster's mantle border with its palps, but I am not sure why, and never witnessed any attack. *Harmothoë* holds its unpaired median antenna curled upwards. It uses its palps to feel. It can hold firmly to its support. Its occurrence on the oyster's cupped valves if the latter are turned downwards proves this. It is sometimes difficult to wash it out of a collecting bottle.

I must confess that I still do not know what the many *Harmothoë* living on the shell of the oyster take as nourishment and whether or not the oyster suffers in any respect from their presence or serve as food to *Harmothoë* in any way. If not, the possibility remains that *Harmothoë impar* is predatory upon other inhabitants of the shell of the oyster. If

this is so we could expect a smaller number of denizens in this habitat in years in which *Harmothoë impar* was particularly abundant, e.g. in the year 1942. One glance at the tables however suffices to demonstrate that species other than *Harmothoë* were normally abundant in that particular year that there is no indication that any species suffered noticeably from *Harmothoë*'s predominance in the year 1942. Therefore all I can say is that *Harmothoë impar*'s means of living is still a mystery to me.

Pholoë minuta FABRICIUS (fig. 4).

Of this small worm, belonging to the subfamily of the Sigalioninae, one juvenile specimen was found during the 1883-'84 zoological survey of the oyster beds in the Oosterschelde (HORST, 1884). Later (1896) HORST, enumerating the Polychaete worms of the Dutch coast, stated that *Pholoë minuta* had been found in the Oosterschelde on oysters, and also near the Isle of Wieringen in the northern part of the former Zuiderzee. In his treatise on the Polychaete worms of the Zuiderzee, HORST (1922) refers again to the finding of one single specimen on an oyster in the Oosterschelde. Though this probably is the same specimen recorded by HORST in 1884, the Leyden Museum of Natural History possesses *Pholoë minuta* collected in the Oosterschelde in 1901 (according to its labelling) which HORST must have known, unless the specimens were acquired much later, which is not indicated.

My investigations revealed that *Pholoë minuta* occurs abundantly on oysters in the Oosterschelde. In fact, I rarely encountered samples of oysters without any *Pholoë* at all. Its favourite site appeared to be the oyster's flat valve, where it hides between the scales of the prismatic layer. Though *Pholoë* is abundant in this habitat, I did not often find it elsewhere in the Oosterschelde. Sometimes I detected a few isolated specimens on tile-collectors bearing oyster spat (Wemeldinge, Tholen). Only occasionally did I find one in samples of bottom material.

I made some observations under laboratory conditions. If forced to choose between oyster-shells devoid of scales and the detached scales, *Pholoë* showed a marked preference for the scales. An oyster of which part of the mantle tissue had been exposed, failed to attract the worm's attention. It appeared to be immaterial to *Pholoë* whether the oysters are placed flat valve upwards or downwards. I could not obtain the slightest indication that it is in any way dependant on the living tissues, rejecta or dejecta of the oyster.

Pholoë minuta is a clear cut case of Polychaete worms coming from the plankton and settling in their favourite habitat, the shell of the oyster. The young oysters with which I started my series, were free of *Pholoë*. Later, small juvenile individuals settled down, increased in numbers,

and started putting on growth in due course. Its occurrence on my experimental oysters can be summarized as follows:

Year	Oysters born in	Period of increase in numbers and predominance of juvenile specimens	Maximum numbers
1941	1940	10/7—31/7, and late in August	2 per oyster
1941	1939	10/7—25/8	5 per oyster
1942	1941	30/6—20/7, and early in August	1 per oyster
1942	1940	30/6—25/8	5 per oyster
1943	1942	21/6—14/7 and 2/8 -20/9	7 per oyster
1943	1941	29/6—14/7	10 per oyster
1944	1943	19/7— 9/8	1 per oyster
1945	1944	25/6— 3/9	3 per oyster

From this it can be concluded that *Pholoë minuta* breeds in summer. Especially in the months of July and August many juvenile individuals left the plankton to settle on the shells of my oysters.

On full grown oysters, taken from the plots of the oystermen, I counted e.g.

p. 417	21-10-1940	15 per oyster
p. 524	4- 4-1941	10 per oyster
p. 211	5-12-1940	12 per oyster
p. 173	7-10-1940	4 per oyster

These figures prove how abundant they are, and also that they occur in different months of the year.

I often encountered larvae of *Pholoë minuta* in my plankton samples. I recorded e.g. 14 specimens taken from 100 liters of water on July 8th, 1941; 12 specimens on August 20th, 1941; 11 specimens on June 15th, 1942; 14 on June 17th, 1942. In very many samples I found from 5 to 10 specimens, but I did not keep a constant record of this. The occurrence of *Pholoë* larvae in the plankton tallies with the appearance of very young individuals on the shells of oysters in the summer season. It is the more surprising to learn that THORSON (1946) during 4 years of plankton investigations in the Sound, did not collect larvae which could be referred to the species *Pholoë minuta*, though this worm abounded on the soft bottom in the Sound. THORSON did frequently find small bottom stages of 1 ½ à 2 mm in July and August, and concluded that *Pholoë minuta* apparently reproduces without any pelagic larval stage in the Sound. I feel sure that THORSON did not overlook the easily recognizable larvae of *Pholoë* in his plankton samples. Could it be that

Pholoë, like so many other species of invertebrates, does not produce planktonic larvae in the colder northern waters? Though not far apart, the Sound is somewhat colder than the Basin of the Oosterschelde. Or do the *Pholoë* of the Sound, living there on a soft bottom, belong to

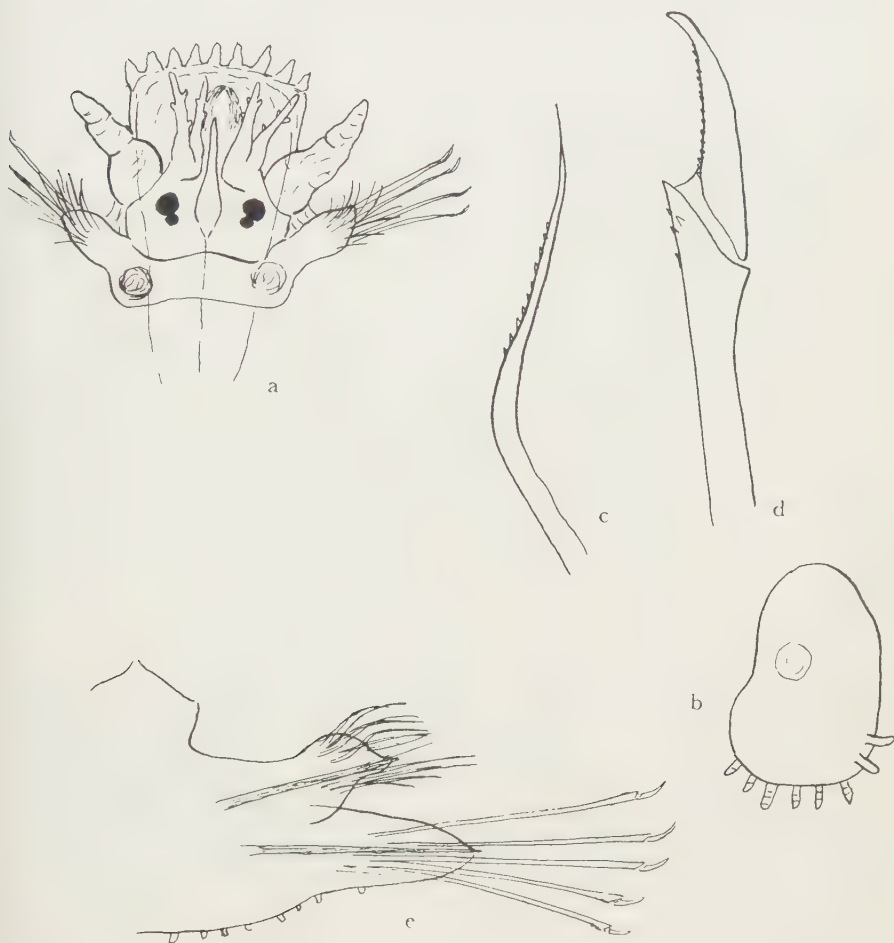


Fig. 4. *Pholoë minuta* FABRICIUS; a. head, dorsal view; b. clytrum; c. neuroseta; d. notoseta; e. parapodium

another subspecies, with a way of reproduction, different from those living on the shells of oysters in the Oosterschelde?

Phyllodocidae:

Phyllodoce maculata (L.)

This lively and lithe Polychaete worm, with its leaflike appendages and its conspicuous rows of dark pigment spots, is common along the Dutch coast. HORST (1884) found it at Wemeldinge. The Leyden Museum possesses several specimens from different localities¹.

I often found it in the Oosterschelde in samples of bottom material rich in shell debris. I also found it rather frequently on oysters. I do not believe, however, that *Phyllodoce* shows a preference for this special habitat, and am inclined to consider it as an occasional visitor rather than as typical of the oyster's epifauna.

The occurrence of *Phyllodoce* on my experimental oysters can be summarized as follows:

Year	Oysters born in	Maximum number
1941	1940	1 per 17 oysters
1941	1939	1 per 10 oysters
1942	1941	1 per 15 oysters
1942	1940	1 per 5 oysters
1943	1942	1 per 50 oysters
1943	1941	1 per 5 oysters
1944	1943	1 per 25 oysters
1945	1944	very few only

I recorded young individuals from 9/6 - 8/7, 1942 and on 8/6, 1943. Data in the literature (c.f. THORSON 1946) indicate that *Phyllodoce* breeds in spring. Could it be that *Phyllodoce* is so scarce on my oysters because I did not put out the trays at Yerseke before May? I do not believe so, for oysters which remained all year on the plots of our oystermen did not have any more *Phyllodoce* than my experimental oysters did. Apparently *Phyllodoce* is not characteristic of the epifauna of the oyster's shell.

Eulalia viridis (MÜLLER).

This worm with its conspicuous colour, often of a brilliant moss-green, sometimes of a duller shade or even brown, which attains fairly large dimensions, is common along the Dutch coast. HORST (1884) found it at Wemeldinge. Many other specimens have been collected since in many a locality (HORST, 1896). It was once collected on the shell of an oyster in the Northern part of the Zuiderzee (HORST, 1920). LELOUP (1940)

¹ Mr P. H. CREUTZBERG has been so kind as to provide me with a list of the Dutch Polychaete worms present in the Leyden Museum of Natural History.

found it in the Bassin de Chasse at Ostend. It is said to breed from January to July inclusive (c.f. THORSON, 1946).

I sometimes found it in samples of bottom material rich in shell debris. It turned up rather frequently in my samples of oysters. It usually hides between the scales of the flat valve. Surprisingly large specimens may find shelter there. *Eulalia viridis*, though not rare on oysters, can hardly be reckoned among the typical representatives of the epifauna of the oyster:

Year	Oysters born in	Occurrence	Maximum numbers
1941	1940	repeatedly	1 per 10 oysters
1941	1939	repeatedly	1 per 12 oysters
1942	1941	very few	1 per 17 oysters
1942	1940	occasionally	1 per 5 oysters
1943	1942	few	1 per 50 oysters
1943	1941	few	1 per 25 oysters
1944	1943	one seen only	
1945	1944	few	1 per 17 oysters

On full grown oysters taken from the plots I sometimes found higher figures. The maximum is: p. 360, 2-10-1940, 3 per oyster. Less frequent, but still worth mentioning was the occurrence of *Eulalia viridis* on samples of oysters from:

p. 835 Ouwerkerk 24-4-1941	20 per 10 oysters
p. 417 Oosterschelde 8-5-1941	11 per 10 oysters
p. 37c Grevelingen April 1941	14 per 10 oysters
Tray in the station Flauwers near Zierikzee 18-10-1940	1 per 5 oysters

The possibility remains that my experimental oysters would have shown a larger number of *Eulalia* if my trays had been kept all the year at the station "Kijk-uit", Yerseke. From November until May I kept the trays with my 2-years old oysters in an oyster basin at Bergen op Zoom, on account of winter risk caused by occasional piling up of ice floes at Yerseke.

Eulalia sanguinea (ØRSTED).

This species is generally considered as rare in Dutch waters (HORST, 1896). The Leyden Museum possesses only 2 Dutch specimens from an unknown locality. DE Vos (1936) found it twice in samples taken in the Zuiderzee.

On my oysters this small and slender worm, with its light nearly transparent pink colour, its glowing yellow eyes, and its quick "nervous" movements, appeared to be more numerous than the bigger *Eula-*

lia viridis. As juvenile specimens prevailed in June and July, I am inclined to conclude that this species breeds in early summer, at least in the Oosterschelde district.

Year	Oysters born in	Period of increase in numbers and predominance of juvenile specimens	Maximum number
1941	1940	10/7	1 per 5 oysters
1941	1939	4/7—31/7	1 per 3 oysters
1942	1941	mid-June—early in July	1 per 3 oysters
1942	1940	22/6—20/7	1 per oyster
1943	1942	few in early summer, light increase late in August	1 per 5 oysters
1943	1941	8/6—29/6	1 per 2 oysters
1944	1943	early in July	1 per 10 oysters
1945	1944	late in June	1 per 5 oysters

I also found it on large oysters taken from the plots of the oystermen, e. g.

p. 417	21-10-1940	1 per oyster
p. 338	24-10-1940	1 per oyster
p. 524	4- 4-1941	1 per oyster
p. 491	25- 4-1941	1 per oyster
p. 210	5-12-1940	3 per oyster
p. 173	7-10-1940	1 per oyster
p. 143	22- 7-1941	2 per oyster

Evidently *Eulalia sanguinea* should be reckoned among the regular inhabitants of the oyster's shell. It can be found there all the year round and more frequently on larger oysters on the beds than on my experimental oysters kept in trays. The greater surface area of the commercial oysters ($\pm 100 \text{ cm}^2$) should however be taken into consideration.

Though I often found one specimen of *Eulalia sanguinea* per oyster, I do not know whether or not this species is predatory on other members of the oyster's epifauna. I could not obtain the slightest indication that *Eulalia sanguinea* depends in any way on the living tissues of the oyster.

Eteone longa (FABRICIUS).

The Leyden Museum of Natural History possesses several specimens of *Eteone longa* collected on the Dutch coast. It has been found e.g. in the Dutch Waddenzee and in the former Zuiderzee (DE Vos, 1936). LELOUP (1940) found it at Ostend in the Bassin de Chasse.

I collected a few specimens in the Oosterschelde:

1 specimen, 18-11-1940 in bottom material from the Zandkreek (Katsche Gat). Further on my experimental oysters:

Year	Oysters born in	Period	Number
1941	1940	July 4	1 specimen only
1941	1939	August 25	1 specimen only
1942	1940	July 14	1 specimen only

And none in my other series.

Eteone longa evidently occurs only occasionally on oysters. I never found it on samples of commercial oysters taken from the plots. From this it may be deduced that its early season of reproduction (c.f. THORSON, 1946) is not the cause of its scarcity on my experimental oysters.

Eteone picta QUATREFAGES (fig. 5).

HORST (1896) stated that he found *Eteone picta* on oysters in the Oosterschelde. Later (1919) he mentioned the finding of this species in the Sloe (Zealand). As HORST expressed some doubt about his own identification and never mentioned the occurrence of *Eteone longa* in Dutch waters, I inquired whether his specimens had been preserved. This appeared to be the case, so that I was able to check HORST's identification. His specimens appeared to belong indeed to *Eteone picta* and not to *Eteone longa*. *Eteone picta* has also been collected in the Waddenzee in recent years (DE VOS, in litt.).

In my plankton samples I came across the larvae of *Eteone picta*, easily recognisable by the lemon-yellow ovoidal anal cirri. I recorded e.g. 6 specimens in 100 liters of water taken in the Oosterschelde on June 17th, 1942, and another specimen on June 19th, 1942.

On my experimental oysters I occasionally found *Eteone picta*, crawling around on the shell:

Year	Oysters born in	Period	Number
1941	1940	July and October	few only
1941	1939	throughout the year	1 per 50 oysters
1942	1941	October 26	1 per 50 oysters
1943	1942	September	a few
1943	1941	occasionally	a few

And none in my other series.

I found more specimens of *Eteone picta* on oysters kept in trays in other stations:

Station Flauwers (near Zierikzee)	18-10-1940	1 per oyster
Station 551, Oosterschelde	21-11-1940	1 per 4 oysters
Station Zandkreek, Katsche Gat	19-10-1940	1 per 3 oysters
Station Stavenisse	7-10-1940	1 per 4 oysters

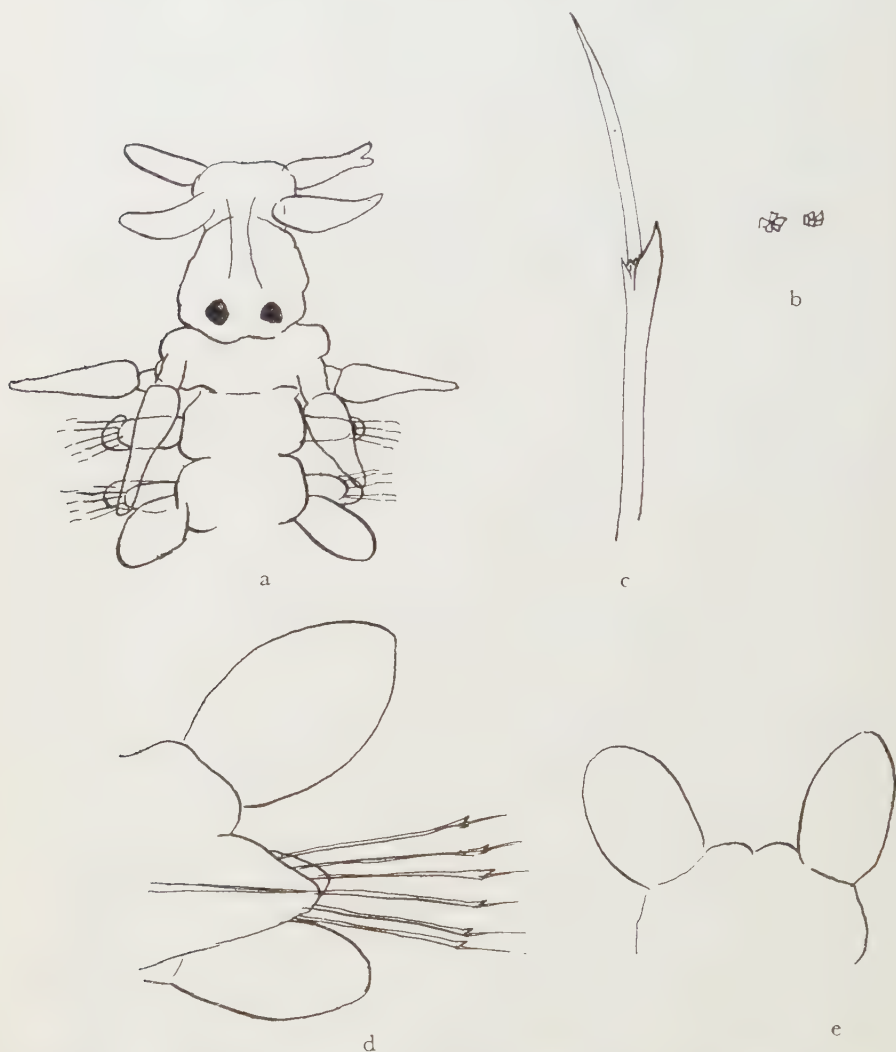


Fig. 5. *Eleone picta* QUATREFAGES; a. head, dorsal view; b. teeth proboscis; c. spinigerous seta; d. parapodium; e. anal cirri

I also collected a specimen in bottom material from the Zandkreek (Katsche Gat).

The year 1940 seems to have been an exceptionally good year for

Eteone picta. In the station "Kijk-uit", Yerseke I found in that year about 1 specimen per 5 oysters during my preliminary survey of the oyster's epifauna. Remarkable is its rather frequent occurrence in the boxes with wire netting of different numbers of meshes per inch (table III).

Both the latter observation and my finding the larvae in plankton samples indicate that *Eteone picta* breeds in summer.

Hesionidae:

Magalia perarmata MARION & BOBRATSKY.

Only once did I find a specimen of *Magalia perarmata*, viz. on August 30th, 1943. I found it on the shell of an oyster born in 1941, kept on a tray at Yerseke from May-October 1942, and then in a tray in the oyster-basin at Bergen op Zoom from October 1942 till August 23rd, 1943. On that day the tray with oysters was transferred to the station "Kijk-uit", Yerseke to replenish my then nearly exhausted stock of 2 years old oysters in that station (c.f. table IX).

The specimen, like most of the Polychaetes collected by me, has been preserved for future reference. As far as I am aware, it is the first *Magalia perarmata* collected on the Dutch coast. Though the possibility remains that this species, not yet recorded from the North Sea, has been imported with oysters from Brittany, the specimen collected was born in the Oosterschelde, as it was found in 1943 on oysters born in 1941, and no Brittany oysters were imported after May 1940.

Syllidae:

Syllis gracilis GRUBE (fig. 6).

This small Syllid worm, with its peculiar beaded cirri and antennae, has been found on the shell of an oyster taken from a regular plot (p. 338) on October 10th, 1940. It has not been recorded before from the Dutch coast, and I did not find it again. It has possibly been brought here with oysters from Brittany.

Exogone gemmifera PAGENSTECHER.

Of this species too but one single specimen has been collected during my investigations. Like the two preceding species it had not yet been recorded from the Dutch coast. We should, however, not attach too much value to this fact, since the Polychaete worms, though highly interesting from a biological point of view, received surprisingly little attention from the Dutch biologists up to this time. I collected my specimen on June 15th, 1943, on an oyster born in 1942, of my regular

series at Yerseke. For reasons explained above this specimen has no doubt been born in the Dutch waters, though the possibility cannot be excluded that its forefathers once were imported with oysters from Brittany or Arcachon. It is remarkable, however, that I have never

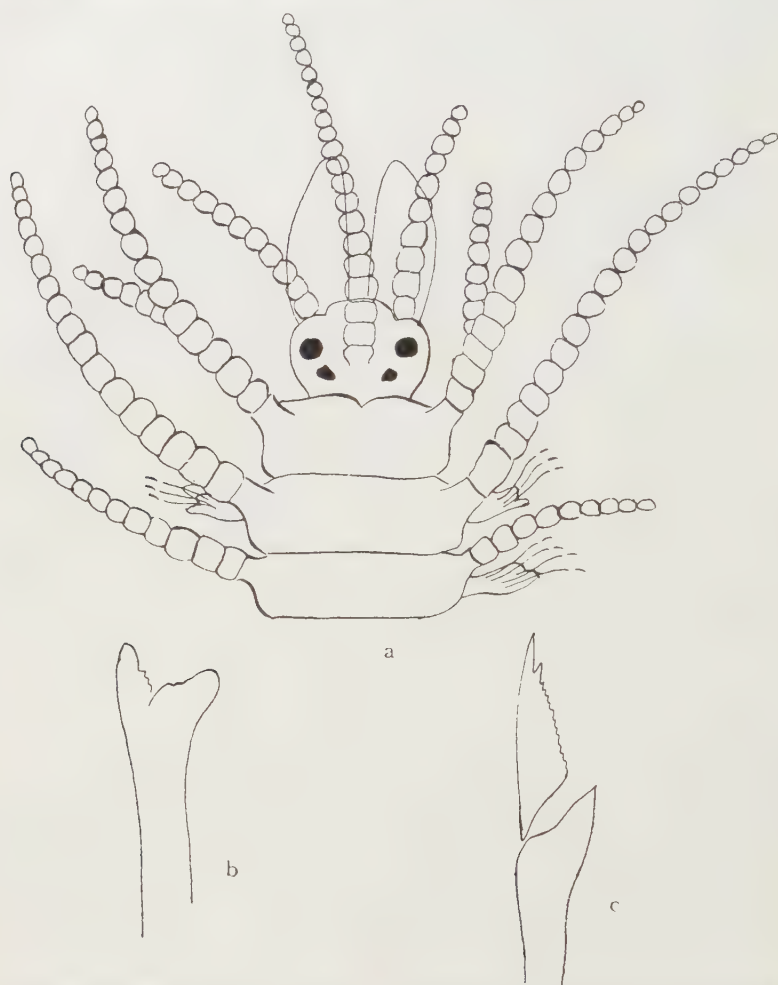


Fig. 6. *Syllis gracilis* GRUBE; a. head, dorsal view; b. hook, middle part of body; c. composite hook, anterior part of body

seen it in years in which fair numbers of French oysters have been relaid in the Oosterschelde. Moreover *Exogone gemmifera* is not a typical southern species.

The specimen concerned was about 2 mm long, possessed 24 segments, and carried several large eggs of a conspicuous purple colour.

One egg was attached ventrally to each parapodium, so that there were 2 per segment. Both dorsal and ventral cirri are very small in this species, which rendered the eggs the more conspicuous.

THORSON (1946) informs us that *Exogone gemmifera* is rather common in the Sound (Denmark). He collected a female specimen bearing eggs in one of his bottle collectors early in July 1941, which tallies with my observation.

Autolytus cornutus AGASSIZ. (fig. 7).

On April 4th, 1941, I found on the shells of large oysters taken from plot 524 Oosterschelde 2 specimens of an *Autolytus* which could not be identified with Fauvel's "Polychètes errantes" (1923). Both individuals measure 7 to 8 mm, and show a fairly dark diffuse brown pigmentation. Behind the head follow 14 setigerous segments, next comes a second head, slightly protruding, followed by 32 and 35 more setigerous segments in my two specimens. The prostomium is rounded. The median antenna is twice as long as the paired antennae, which are smooth and set between the foremost eyes. The palps protrude slightly. There are 4 eyes bearing a crystalline lens and 2 small eye-spots in front of them. The retracted proboscis is S-shaped. The dentition consist of a "trepan" bearing 16 teeth of equal length, but alternately broader and narrower. The proventriculum (gizzard) is ovoidal, smooth, and placed in the segments 3 and 4. The dorsal peristomial cirri are somewhat shorter than the paired prostomial antennae. The ventral peristomial cirri are short. The dorsal cirri of the first setigerous segment are very long, about $\frac{3}{4}$ of the length of the median antenna. The dorsal cirri of the other segments are short and of equal size and shape. There are 2 short anal cirri. The composite hooks have a broad appendage, distally bidentate. The parapodia bear several spinigerous setae.

OKADA's paper (1933a) made it clear to me that my *Autolytus* belongs to the species *A. cornutus* AGASSIZ. OKADA claims that this is an American species, recently introduced in the Plymouth area, and probably transported attached to Hydroids on a ship's bottom. OKADA did not find this species during his investigations at Plymouth in June 1927. In June 1929 it appeared to abound there, especially on *Laminaria* covered with the Hydroid *Obelia*. Of one species of *Autolytus* it has been observed that they feed on Hydroids (OKADA 1928). Therefore transportation on the Hydroids of a ship's bottom is assumed.

If it is true that *Autolytus cornutus* has been introduced at Plymouth between 1927 and 1929, and the fact that neither FAUVEL nor other authors mentioned this species for the European waters supports this view, we can add that it has reached the continent now.

Apart from the individuals mentioned above, I came across several other specimens of *Autolytus cornutus*. From my experimental oysters the following individuals have been recorded:

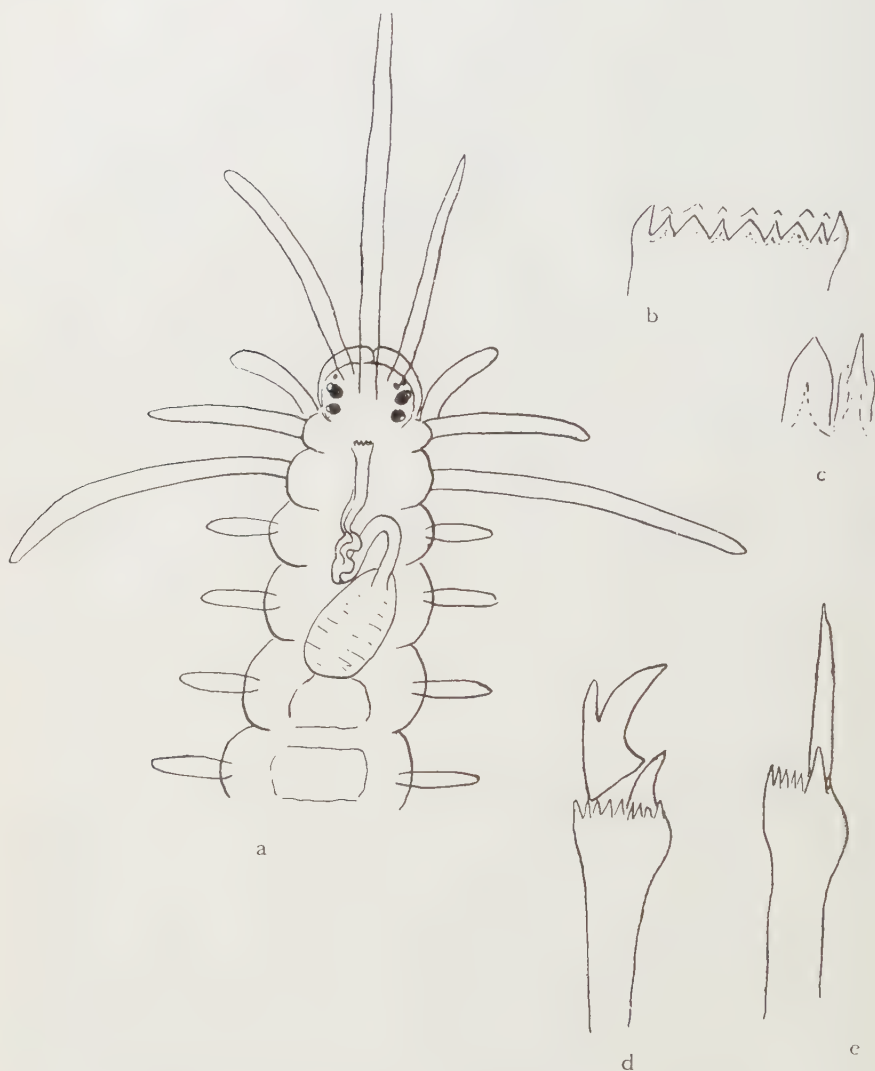


Fig. 7. *Autolytus cornutus* AGASSIZ; a. anterior part, dorsal view; b. trepan; c. teeth, greatly enlarged; d. composite falcigerous seta; e. composite spinigerous seta

Year	Oysters born in	Period
1941	1939	25/6, 4/7, 10/7, 17/7, 25/8
1942	1941	30/6 (2), 8/7 (2), 20/7 (3)
1942	1940	8/7, 14/7, 20/7
1943	1941	25/6, 21/6 (2)

And none on other series.

On oysters from the plots I found it:

p. 524	4-4-1941	2 on 25 oysters
p. 491	25-4-1941	1 specimen
p. 37c Grevelingen	April 1941	1 specimen

Though *Obelia* is a common species in the Oosterschelde, I did not find it on my experimental oysters. I therefore doubt whether my specimens could have lived on a diet of *Obelia*. No other Hydroids occurred in appreciable numbers on my oysters during the time I found *Autolytus cornutus*.

Autolytus aurantiacus (CLAPARÈDE) (fig. 8).

Even during my 1940 preliminary survey of the oyster's epifauna I frequently met a species of *Autolytus* which was difficult to identify. I learned later that this species is so abundant on oysters in the Oosterschelde, that it can be reckoned among the characteristic inhabitants of this special habitat. I never found it elsewhere.

As the material collected by me did not seem to be identical with any of the members of the genus *Autolytus* listed by FAUVEL (1923), I invoked the assistance of this famous specialist. Professor FAUVEL kindly drew my attention to the great resemblance to *Autolytus aurantiacus* (CLAPARÈDE). There were differences, however. I always counted from 30 to 45 setigerous segments, even in the individuals bearing stolons. *A. aurantiacus* should possess 60 – 100 segments. Mine always had 22 – 24 teeth on the "trepan". *A. aurantiacus* should have 16 – 20 teeth. I observed a very peculiar sequence in the length of the dorsal cirri, not mentioned in *A. aurantiacus*. Moreover my specimens were invariably collected on the shells of oysters, a habitat not mentioned for *A. aurantiacus*. I was therefore on the point of describing my material as a new species. Doubt arose when Prof. FAUVEL informed me that the number of segments may vary greatly with size and age of the animals. My specimens rarely reached 12 mm, while 20 mm is given for *A. aurantiacus*. I was also informed that the number of teeth is not strictly constant and may show a variation of 3 or 4. When I found then an individual of 15 mm long with 68 segments, and found that the number

of teeth was not always 23 or 24, but could be as low as 20, and that every third tooth is somewhat stouter, I was inclined to agree that my material belonged to the species *A. aurantiacus* (CLAPARÈDE), and at most represented a geographical or biological race.

It is desirable to give here a detailed description of my material: Body slender, with 30 to 45 setigerous segments in individuals of about 10 mm long. A specimen of 15 mm had 68 segments. Prostomium round, broader than long, with 4 large eyes, bearing a crystalline lens, and placed trapezium-wise. Sometimes 2 additional eye-spots. Median antenna, set between the foremost eyes, twice as long as the paired prostomial antennae. Palps slightly protruding, clearly visible. Retracted proboscis crowned with a "trepan" bearing 20 - 24 teeth of equal length, every third tooth somewhat broader than the others (c.f. FAUVEL 1923, fig. 120c, p. 313). Proventriculum (gizzard) ovoidal, bearing about 40 rows of points, situated in the segments 8 - 11. Dorsal peristomial cirri as long as the paired prostomial antennae. Ventral peristomial cirri shorter. Antennae and cirri bearing minute spines, barely visible. Dorsal cirri of the first setigerous segment at least as long as the median prostomial antenna. Dorsal cirri of the second setigerous segment somewhat shorter than the paired prostomial antennae. Dorsal cirri of the 3rd setigerous segment about half as long as those of the 2nd. Those of the 4th, 6th, 9th, 11th, 13th, 15th, 17th, 19th, 21st, 23rd, 25th, 27th, 30th, 31st, 34th, 35th setigerous segment of about equal length with those of the 2nd setigerous segment. Dorsal cirri of the 3rd, 5th, 7th, 8th, 10th, 12th, 14th, 16th, 18th, 20th, 22nd, 24th, 26th, 28th, 29th, 32nd, 33rd setigerous segment of about equal length, and half as long as the above-mentioned cirri. Cylindrical cirrophores. 2 long anal cirri. Composite falcigerous setae distally bidentate. The posterior segments possess one finely pointed spinigerous seta.

Most of the individuals collected measured about 5 to 10 mm.

Colour pale pinkish, sometimes with light red spots, as described for *A. aurantiacus*. *Polybostrichus*: first 3 segments with composite setae only, followed by 19 segments with additional swimming bristles. Colour a conspicuous blueish green.

Sacconereis: Median antenna only slightly longer than the paired antennae. 2 Peristomial cirri. Dorsal cirri of gradually diminishing length from head to tail. 2 long anal cirri. The first 2 setigerous segments with composite setae only, followed by 17 segments of which all but the last bear additional swimming bristles. Body crammed with eggs from head to tail. Colour pale pinkish.

The occurrence of *Autolytus aurantiacus* on my experimental oysters can be summarized as follows:

Year	Oysters born in	Period of increase in numbers	Maximum number
1941	1940	10/7	1 per 2 oysters
1941	1939	25/6 — 4/7	1 per oyster
1942	1941	16/6 — 14/7	1 per 2 oysters
1942	1940	22/6 — 20/7	1 per oyster
1943	1942	8/6 — 30/6	1 per 2 oysters
1943	1941	15/6 — 29/6	2 per oyster
1944	1943	22/6 — 28/6	1 per oyster
1945	1944	25/6	1 per 2 oysters

It also occurred in other stations:

a) On oysters kept in trays:

p. 421	25- 9-1940	2 per oyster.	<i>Polybostrichus</i> and <i>Sacconereis</i> present
Stavenisse	7-10-1940	1 per oyster	
Dortsman	7-10-1940	1 per 2 oyster	<i>Polybostrichus</i> numerous (oysters born in 1941 and bearing many barnacles)
p. 551	21-10-1940	2 per oyster.	
p. 421	22- 7-1941	6 per oyster	

Zandkreek 23- 8-1941 1 per oyster

b) On commercial oysters taken from the plots:

p. 491	25- 4-1941	1 per oyster
p. 143	22- 7-1941	1 per oyster
p. 200	14- 8-1941	2 per oyster

I never found this *Autolytus* on tile collectors or in samples of bottom material. This does not exclude its presence in other special habitats, not closely investigated by me.

Mature stolons have often been observed, especially on June 15th, 1943. *Sacconereis* stolons were numerous. Even while still attached to the crawling adult, the stolons may start swimming. Also in plankton samples I often encountered the *Polybostrichus* and *Sacconereis* stolons of this *Autolytus*. I recorded them on June 23rd, 1943 and July 11th, 1941.

From this and from my tables it can be deduced that *Autolytus aurantiacus* reproduces especially in the month of June. Individuals bearing *Polybostrichus* stolons have been observed in other months too (September, October).

It would be interesting to know why *Autolytus aurantiacus* shows such a marked preference for the habitat under consideration. If observed in vitro it often makes a thin hyaline tube, attached horizontally to the glass wall close to the meniscus. It can stay there for many days without food. Similar hyaline tubes are also made on the shells of the oyster, both on the cupped and on the flat valve.

Tiny oyster spat or oysters of which part of the mantle tissue had

been exposed, failed to attract the attention of *Autolytus*. Living barnacles did not interest them either. Prolongued fasting did not change its behaviour towards oysters or barnacles. The finding of a very great

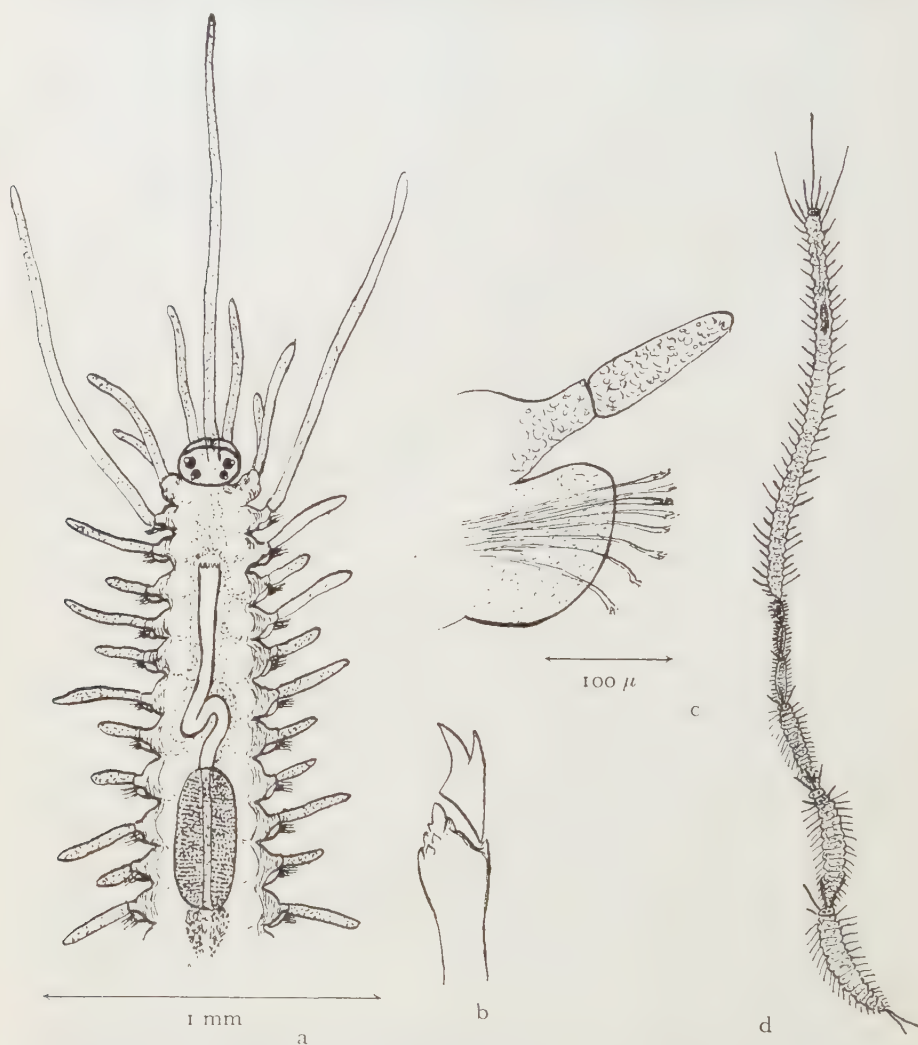


Fig. 8 A. *Autolytus aurantiacus* (CLAPARÈDE); a. anterior part, dorsal view; b. composite falcigerous seta; c. parapodium; d. adult individual with stolons

number of *Autolytus* on the oysters covered with barnacles in the tray on plot 421, suggested that *Autolytus* might be interested in them.

OKADA (1928) described in detail the feeding behaviour of *Autolytus Edwardsi* ST. JOSEPH. This species appeared to feed on the hydranths

of *Obelia*. After several days of fasting *Autolytus* attacked the hydroid very eagerly, which gave OKADA the opportunity of studying its feeding behaviour in detail. He observed that the nematocysts of the Hydroid

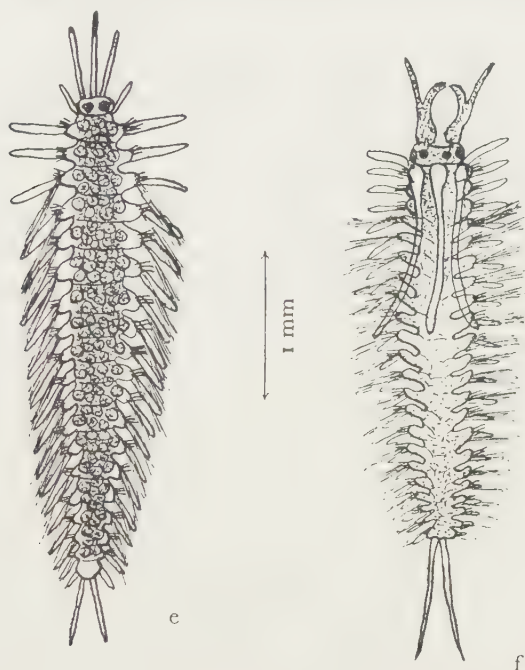


Fig. 8 B. e. female stolon (*Sacconereis*); f. male stolon (*Polybostrichus*)

apparently did not hurt *Autolytus Edwardsi*; it just shakes its head and frees itself without any apparent injury.

Hydroids were so scarce on my oysters (as can be seen in the tables) that I can hardly believe that *Autolytus aurantiacus* feeds on Hydroids. Could it be that the polyps of *Aurelia aurita*, often so numerous on my oysters, are attacked by *Autolytus*? In the laboratory *Autolytus* did not show any interest in the polyps of *Aurelia*, not even after prolonged fasting, or in the dark. If it touches the polyps accidentally, and the latter defend themselves with their nematocysts, *Autolytus* shrinks back and proceeds on its way without apparent injury. Oysters bearing many polyps of *Aurelia*, usually bear the normal number of *Autolytus*.

It is still a mystery to me what *Autolytus aurantiacus* eats. Hydroids being rare on my oysters, and polyps of *Aurelia* apparently not attractive to it, could it be that the Bryozoan *Barentzia gracilis*, sometimes present in appreciable numbers, forms its food? I doubt it.

It is remarkable that the occurrence of several species of *Autolytus* on

oysters has been recorded by other authors. FAUVEL (1923) mentions the finding of *A. megodon* ST. JOSEPH on old oyster shells near Dinard (Brittany), and of *A. paradoxus* ST. JOSEPH on oysters dredged in the Channel and Straits of Dover. *Autolytus aurantiacus* has been found as far North as Dunkirk, but oysters are not mentioned in this connection. OKADA (1933b) described *A. purpureimaculatus* found on living specimens of *Ostrea gigas* THUNBERG. OKADA speaks of its semiparasitic mode of life. Upon my request OKADA informed me, however, that he had not the slightest proof that *A. purpureimaculatus* really lives parasitically on the oyster: "I must confess that I have no concrete knowledge about its biological habits, beyond that the animals are easily obtained, any time of the warmer season, by placing fresh, recently collected oysters into a large wooden or porcelain vessel filled with ordinary sea water. Waiting then for several hours, sometimes half a day, the *Autolytus* begins to creep about on the shell of the oyster. I do not know where they come from. The *Autolytus* must live somewhere outside the shells. Since, however, they are always closely associated with living oysters, I suppose that they live on the latter, perhaps sometimes enter the mantle cavity and suck nutritive fluids there". (OKADA, 1941, in litt.).

If that is proof enough, I have just as much right to assume a semiparasitic style of living for many of the animals I found on the shells of living oysters. They are associated with living oysters, and I do not know what they eat. I never observed one entering the oyster's mantle cavity to feed, however. Only after a prolonged sojourn out of water some Polychaete worms (especially *Eulalia viridis* and *Nereis succinea*) may crawl in between the slightly gaping shells of the oyster, probably in search of moisture.

I assume that OKADA's *Autolytus purpureimaculatus* lives hidden between the scales of the flat valve of his oysters, as so many creatures do on the shells of our *Ostrea edulis*. Either by lifting the scales under water, or by placing the oyster in a little sea water until the oxygen supply becomes exhausted, we may find these interesting creatures, about which we still know so little.

Nereidae:

Nereis diversicolor O.F. MÜLLER.

This fairly large worm is common along the Dutch coast. Since HORST (1884) found a specimen in the mud of the Bergen op Zoom harbour, a great many others have been collected, especially in the Waddenzee and in the Zealand streams. HORST himself (1896, 1922) labelled this species as "not rare". LELOUP (1940) records its occurrence in the Bassin de Chasse at Ostend. It is a very euryhaline species, which

usually lives in deposits rich in mud. I collected several specimens in and near the tidal basin at the station "Kijk-uit", Yerseke (e.g. 20-11-1940). Though it abounded in this station I never found one on the shells of my experimental oysters there.

Only once did I find a small specimen of *Nereis diversicolor* on an oyster: p. 551, 21-10-1940. The species apparently does not like that habitat. In samples of bottom material, on the other hand, I often encountered *Nereis diversicolor*. The soft mud of the Katsche Gat, Zandkreek, appeared to be especially rich in this species (18-11-1940).

Nereis succinea (LEUCKART).

This worm, easily recognizable by the leaflike enlarged dorsal lobes of its posterior segments, was considered rare on the Dutch coast by HORST (1896). Later (1922), he found it rather frequently in samples taken in the former Zuiderzee. The Leyden Museum possesses many specimens collected in the Zuiderzee in August 1905. Recently it has been found in many bottom samples taken in the Waddenzee (DE Vos, in litt.). LELOUP (1940) collected it in the Bassin de Chasse at Ostend.

Though the normal habitat of *Nereis succinea* is said to be a sandy mud, in which I collected it on several occasions (Kattendijke 25-10-1940; p. 188 3-12-1940; Bergen op Zoom 29-11-1940), small specimens live occasionally on the shells of oysters. From the following summary drawn from the tables, it can be concluded that *Nereis succinea* is not very common on my experimental oysters:

Year	Oysters born in	Period of increase in numbers	Maximum number
1941	1940	July, mid-August	1 per 3 oysters
1941	1939	mid-July, mid-August	1 per 4 oysters
1942	1941		very few
1942	1940	July 22nd	2 specimens only
1943	1942	late summer	few only
1943	1941	late summer	very few
1944	1943	August	few only
1945	1944		not seen

On trays with oysters placed in other stations I found it too, especially in the year 1941, which seems to have been a good year for *Nereis succinea*:

Flauwers (near Zierikzee)	18-10-1940	2 per 25 oysters
Zandkreek (Katsche Gat)	19-10-1940	3 per 25 oysters
p. 421	22- 7-1941	5 per 25 oysters
	9- 8-1941	3 per 25 oysters
Bergen op Zoom, oyster basin	20- 8-1941	5 per 25 oysters
Yerseke, Harden Hoek, tidal basin	21- 8-1941	5 per 25 oysters
Kattendijke, tidal basin	15- 8-1941	8 per 25 oysters

I also found it on oysters taken from the plots of the oystermen:

p. 200	24- 8-1941	4 per 25 oysters
p. 212	30- 7-1941	4 per 25 oysters
p. 388	24-10-1940	2 per 10 oysters
p. 524	4- 4-1941	2 per 25 oysters
p. 835 Ouwkerk	24- 4-1941	2 per 25 oysters
p. 467	22-11-1940	4 per 20 oysters
p. 252	24-10-1940	2 per 10 oysters

I also found some in the boxes with wire netting placed at the station Yerseke in the year 1940 (table III).

Though it cannot be claimed that *Nereis succinea* is characteristic for the epifauna of the oyster's shell, its occurrence is too frequent to call it just an incidental visitor.

Nereis virens (SARS).

This giant among the Dutch Polychaete worms attracts attention by its swarming. Many then leave their burrows simultaneously and swim about, displaying their beautiful metallic colours in which green dominates. It has been found in several places along the Dutch coast, especially in Zealand and in the Waddenzee. LÉLOUP (1940) found it at Ostend.

It occurs in great numbers in the bottom deposits rich in stones and debris in the tidal basin at the station "Kijk-uit", Yerseke. Local fishermen sometimes dig it for bait. In bottom material from p. 188 I found a specimen of 12 mm only (3-12-1940). It is my impression that *Nereis virens* likes places rich in stones and avoids pure clean mud.

I never found young individuals on oysters. The swarming of this big *Nereis* is a conspicuous phenomenon. There are indications that swarming takes place at spring tide in April (KORRINGA 1947). I witnessed its swarming at Tholen during the new moon spring tide of April 1946. Several other individuals have been collected at spring tides in April, but not exclusively during the new moon spring tides. Though it lives close at hand, and is both large and conspicuous, we know far less about its swarming rhythm than we do about swarming in the Palolo worm of the Pacific.

Nereis longissima (JOHNSTON).

This species has been collected in several stations along the Dutch coast. HORST (1884, 1896) classed it as "not rare". It has repeatedly been washed ashore between Den Helder and Scheveningen (Leyden Museum). Several specimens have been collected recently in the Waddenzee (DE VOS, in litt.). LÉLOUP found it in the Bassin de Chasse at Ostend.

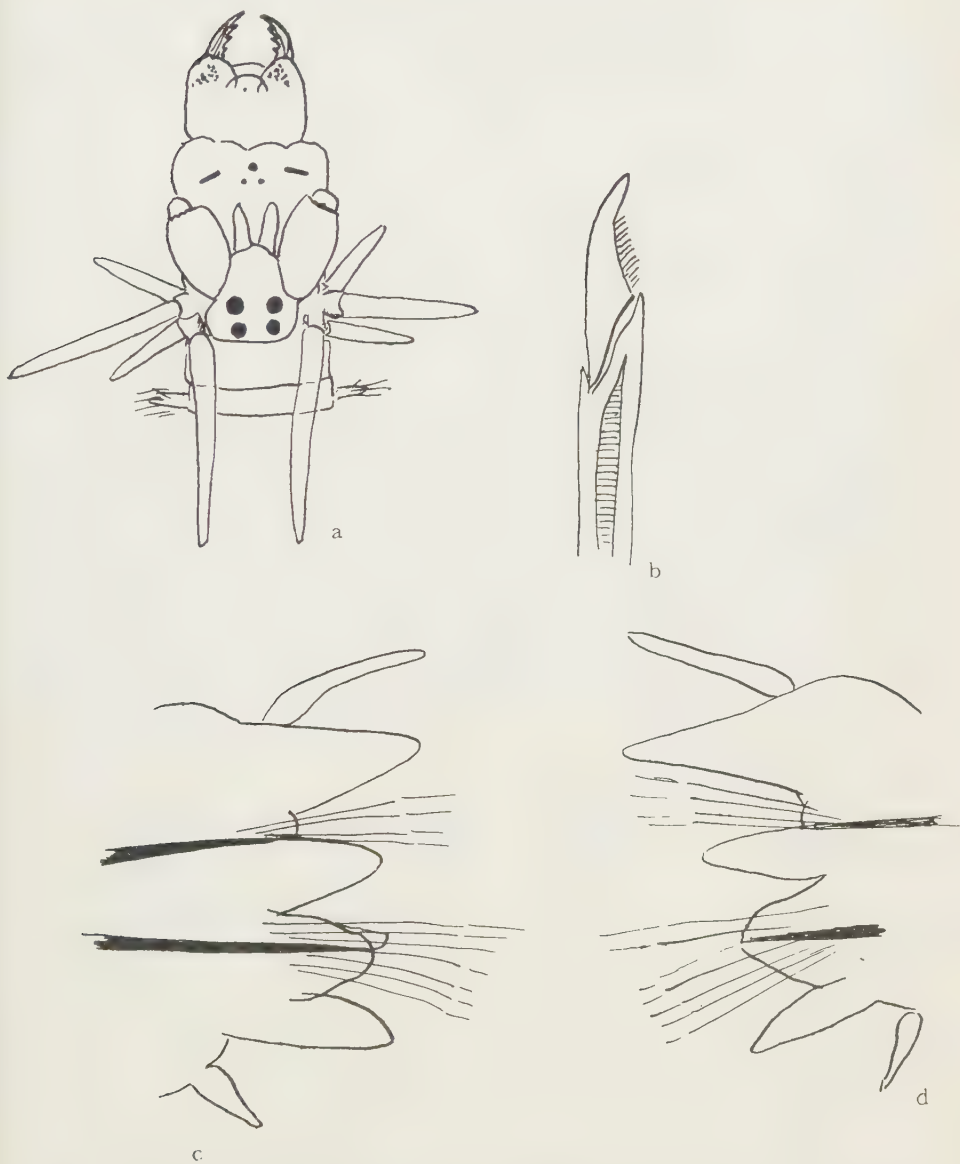


Fig. 9. *Perinereis cultifera* (GRUBE); a. head, proboscis extruded, dorsal view; b. composite hook; c. anterior parapodium; d. posterior parapodium

I found a small specimen of *Nereis longissima* on the shell of a living oyster taken from a regular plot (p. 230 Hammen, near Zierikzee) on October 7th, 1940. Recently (20-1-1950) I came across another specimen, measuring 20 mm, on the shell of an oyster from the Yerseke Bank, Oosterschelde.

Perinereis cultrifera (GRUBE) (fig. 9)

One single specimen, measuring 29 mm, has been collected by me on tile-collectors near Wemeldinge (25-10-1940). I know of no other Dutch records.

Platynereis Dumerilii (AUDOUIN & M. EDWARDS) (fig. 10).

HORST (1884, 1896, 1922) claimed that *Platynereis Dumerilii* was rare in Dutch waters. It has been found in the Oosterschelde and once in the Northern part of the Zuiderzee. Only a few specimens have been collected since (washed ashore at Texel; Leyden Museum). FERRO-NIÈRES (1901) found *Platynereis* in oyster parks at Le Croisic. GRAVIER (1900) claims that *Platynereis Dumerilii* has been found in oysters, and therefore classifies this species as a temporary commensal. I doubt, however, whether the specimens studied by GRAVIER were really collected inside the oyster's shell, and not from the shell's exterior surface.

Occasionally I found *Platynereis Dumerilii* on my experimental oysters:

Year	Oysters born in	Period	Abundance
1941	1940	October/November	regularly
1941	1939	August-October	few only
1942	1941	October	very few
1942	1940	late in September	very few
1943	1942	September/October	regularly
1943	1941	September/October	occasionally
1944	1943		very few only
1945	1944		very few only

I also found this species on oysters taken from the plots:

p. 338	24-10-1940	2 per 10 oysters
p. 524	4- 4-1941	10 per 25 oysters
p. 210	5-12-1940	4 per 10 oysters
p. 173	7-10-1940	7 per 25 oysters
p. 339	7-10-1940	10 per 25 one-year old oysters

I found them also on oysters kept in trays other than my regular series:

p. 551	21-10-1940	3 per 25 oysters
Yerseke	10-10-1940	10 per 50 oysters

Moreover it occurred fairly frequently in the boxes with wire gauze, placed at Yerseke in the year 1940 (table III).



Fig. 10. *Platynereis Dumerilii* (AUDOUIN & M. EDWARDS); a. head, dorsal view; b. teeth, group IV proboscis; c. homogomph falcigerous neuroseta posterior segments; d. heterogomph falcigerous notoseta; e. posterior parapodium; f. anterior parapodium

New individuals of this species apparently made their appearance in September and October. Did they come from the plankton?

HEMPELMANN (1911) demonstrated that *Platynereis Dumerilii* may

produce both "neridogene" and "planktogene" larvae, the latter from epitocous parents. THORSON (1946) never found *Platynereis* larvae in his plankton samples, though adult specimens abound in the Sound. He assumes that only "neridogene" larvae are produced there. As I cannot remember ever having seen a larva of *Platynereis* in my plankton samples, and as the new individuals found on my oysters are not always very small ones, I am inclined to support THORSON's assumptions. My data suggest that oysters from the plots may carry more individuals of *Platynereis* than those kept on trays, but the difference is not very significant, and the oysters taken from the plots usually had a larger surface area than those kept on trays.

Platynereis Dumerilii can easily be kept in the laboratory, where it makes hyaline tubes to hide in against the glass walls of a jar. It would eat *Ulva* and some other sea-weeds, and presumably should be reckoned among the herbivores. It usually has a beautiful colour: light green with violet chromatophores.

I found very many and very large specimens on tile-collectors in the wintering pits near Yerseke (7-4-1943). In taking the tiles apart, many of the worm's tubes, hidden by some accumulated mud, were ruptured, which made it easy to collect the worms themselves. I also collected a great number among oysters and shells in the oyster-basin at Bergen op Zoom (8-6-1945). In the Oosterschelde it is not at all rare. Its importance as a member of the oyster's epifauna is limited, however.

Nephtydidæ:

Nephtys Hombergi AUDOUIN & M. EDWARDS.

Nephtys Hombergi has been collected in the Oosterschelde by HORST (1884), and is common in many places along the Dutch coast (HORST 1896, 1922). Many Dutch specimens are preserved in the Leyden Museum. It frequently turned up in bottom samples taken in recent years in the Waddenzee (DE VOS, in litt.). LELOUP records it from the Ostend Bassin de Chasse.

I encountered it several times in the Oosterschelde, e.g. in samples of bottom material taken from the stations: "Kijk-uit", Yerseke (6-10-1940); p. 551 (21-5-1941); p. 188 (3-12-1940). While wading on the oyster plots near the low water line, I occasionally caught a swimming *Nephtys*: p. 70 (13-5-1941), p. 98 (16-5-1941). I never found it on oysters.

Ariciidae:

Scoloplos armiger (O. F. MÜLLER)

This worm occurs in numbers in the superficial bottom layers at many places on the Dutch coast. HORST (1896) calls it fairly common. He

later (1922) records it from the Sloe (Zealand) and collected the species near the Isle of Wieringen. DE Vos (1936) found some specimens in material collected in the Zuiderzee. Many specimens have been collected recently in the Waddenzee (DE Vos, in litt.). The Leyden Museum possesses many Dutch specimens. LELOUP (1940) found it at Ostend.

I often found it, sometimes in great numbers, in bottom samples taken in the Oosterschelde, e.g.:

p. 486 27- 4-1941

p. 551 21- 5-1941

p. 188 3-12-1940

"Kijk-uit", Yerseke 6-11-1940

In early spring the green, gall-bladder like capsules containing the eggs of *Scoloplos* can be seen on the oyster plots close to low-water mark. Though these egg-capsules are not very large, our fishermen know them very well, a proof that they are fairly abundant.

I once found a juvenile specimen of *Scoloplos armiger* on the shell of an oyster: 20-5-1941, Yerseke, "Kijk-uit", on oysters born in 1939. This individual, living between the scales of an oyster's flat valve, had perforce to be satisfied with a very little bit of its natural habitat: a sandy mud.

Spionidae:

Polydora ciliata (JOHNSTON) (fig. 11).

If the question is put which Annelid occurs in greatest numbers in the Dutch coastal waters, I am inclined to answer: *Polydora ciliata*. It is the more surprising that HORST (1884) did not mention it from the Oosterschelde. This must have been an omission, since it had already attracted BASTER's attention there (1759), and since HOEK (1902) found it so abundantly on the oyster beds of the Oosterschelde. It is no doubt very common on the Dutch coast (HORST 1896). It does not always live in shells and other calcareous material, but also most abundantly in peat-bottoms (e.g. in the Waddenzee; DE Vos, in litt.).

I found it frequently on my experimental oysters, practically exclusively between the scales of the flat valve's prismatic layer. There it appeared to have constructed its burrows, in which I sometimes found its strings of egg-sacs. Extensive accumulations of mud, brought there by *Polydora* itself, surrounded the burrows in which the worm lived. Often *Polydora* extends its burrow beyond the scales of the oyster's flat valve. That part of the burrow is not just a rough accumulation of mud with a hole inside, such as we found between the scales, but a neat round tube of a gray colour. This tube may be short or long. Under water, *Polydora* protrudes with its long, extensible palps from the end of

the tube in search for food, which it takes from the surrounding sea-water. Our knowledge of *Polydora*'s food collecting mechanism is still far from complete. We do not know the smallest size of particles it can catch, and how it does that. I assume that *Polydora* always tries to ensure good communication with the surrounding sea-water. If the position of its substratum (here an oyster) becomes unfavourable, *Polydora* can lengthen its tube considerably in an effort to reach open sea-water. Usually *Polydora ciliata* living between the scales of the oyster's flat valve does not make a U-shaped burrow, but just follows the slightly curved line of attachment of those scales.

The occurrence of *Polydora ciliata* on my experimental oysters can be summarized as follows:

Year	Oysters born in	Period of increase in numbers and predominance of juvenile specimens	Maximum number
1941	1940	16/6-24/7	1 per 2 oysters
1941	1939	20/6- 4/7	1 per oyster
1942	1941	9/6-14,7	1 per oyster
1942	1940	9,6- 8,7	1 per oyster
1943	1942	2,6-29,6	1 per 2 oysters
1943	1941	8,6-21,6	1 per oyster
1944	1943	22,6	1 per 3 oysters
1945	1944	17,5	1 per oyster

In many cases the number of *Polydora* encountered on the flat valve decreased noticeably later in the season (1941, 1942, c.f. the tables). Can it be, that sooner or later several of them fall victim to predatory Polychaetes living in the same habitat? The mud-burrows between the scales of the oyster's shell do not offer complete protection.

From the data tabulated above it can be concluded that young *Polydora* settle down in great numbers in the month of June. Usually some individuals were found very soon after I placed my trays with oysters in the basin at Yerseke (last ten days of May), which indicates that reproduction of *Polydora* was already in full swing. This is in agreement with information on its season of reproduction at Kiel (April-October, with a maximum in July) and in the Sound (April-September; THORSON 1946).

The larvae of *Polydora ciliata* are numerous in plankton samples taken in The Oosterschelde, especially in the month of June. Often from 30 to 70 *Polydora* larvae could be counted in 100 liters of water, which corresponds with about 250,000,000,000 larvae in the Bassin of the Oosterschelde. It is by far the most abundant Polychaete larva in the

summer plankton of the Oosterschelde. The larvae are said to be very voracious and omnivorous, and the larger ones may feed on Lamelli-branch larvae too. Considering their abundance, it can be taken for granted, that they cause considerable losses among the oyster larvae.

I also found *Polydora ciliata* between the scales of the flat valve of oysters taken from the regular plots:

p. 835 Ouwerkerk	24- 4-1941	more than 100 per 25 oysters
p. 467	22-11-1940	more than 100 per 25 oysters



Fig. 11. *Polydora* in oyster shells. a. burrows of *Polydora ciliata* (JOHNSTON) in cupped valve of *Ostrea edulis*. Partly sealed off with circular patches of conchyolin; b. burrows and mud deposits of *Polydora hoplura* in cupped valve of *Ostrea edulis*, seen in transmitted light. One sealed off with large patch of conchyolin

Usually, however, I counted only from 10 to 15 specimens per 25 large oysters. I also found it on oysters kept in trays in several stations in the Oosterschelde:

p. 551	21-10-1940	2 per oyster
Flauwers, near Zierikzee	18-10-1940	60 per 25 oysters
Zandkreek, Katsche Gat	23- 7-1941	1 per oyster
Bergen op Zoom. . . .	20- 8-1941	1 per oyster
Bergen op Zoom. . . .	22- 7-1942	1 per oyster

It was moreover fairly numerous in the boxes with wire gauze used at Yerseke in the year 1940 (table III). In the boxes in which the gauze was of 40 or 50 meshes per inch, their number was not smaller than in those with coarser wire netting. Apparently *Polydora* larvae do not hesitate to crawl through narrow apertures.

SCHODDUYN (1931) also mentions the occurrence of *Polydora ciliata* on oyster shells, where it usually lives in tubes between the scales of the flat valve.

Only once did I come across a description of serious damage caused by *Polydora* living between the scales of the oyster's flat valve:

LELOUP (1937, 1940) records serious losses among relaid Dutch oysters, caused by *Polydora ciliata*, in the Bassin de Chasse at Ostend. In this Basin with stagnant water *Polydora ciliata* is so abundant, that the bottom is really plastered with its tubes. This is an exceptional case. In places along the coast where considerable wave activity and strong currents prevail, the abundance of, and damage done by, *Polydora* to oysters and *Littorina* is very limited, according to LELOUP. "Il semble que les larves des Polychètes perforateurs aient peu de chance de se fixer sur des coquilles constamment brassées par le flot." In the Bassin de Chasse, where *Polydora ciliata* was so extremely numerous, many worms settled on the flat valves of the relaid oysters. The result was, that the oyster could not put on any growth on the edge of its flat valve. The cupped valve only, being free of *Polydora*, could produce a new shoot. As the edge of flat and cupped valve must fit together, the result was, according to LELOUP, that the oysters curled the edge of the cupped valve upwards, in an effort to join the flat valve, which could not be enlarged. LELOUP adds that this finally caused the oyster's death, as the new position of the shell aperture brought about a condition in which too much silt and debris, deposited by *Polydora*, found its way inbetween the oyster's valves.

LELOUP ascribes the failure of the flat valve to put on any growth to the burrowing action of *Polydora*, by which the calcareous layers of the shell finally become scaled off: "Ils desquament les couches calcaires et le bord de la valve devient tres friable. Comme l'huître ne parvient pas à réparer les dégâts sans cesse renouvelles, la valve droite subit un arrêt de croissance. Pendant ce temps la valve gauche bombée continue à s'accroître et, dans sa tendance à rejoindre la valve opposée, que ne lui offre pas de résistance, se recourbe vers le haut."

I can add that the extreme edge of the oyster's flat valve consists of the elastic prismatic layer. Only by adjusting the hard calcareous border of the cupped valve against this elastic material can the oyster obtain the the necessary perfect closure. As the newest scale of the prismatic layer is broadened, harder calcareous layers are deposited against its base. It can be assumed that too vigorous an action of a multitude of *Polydora* living between the scales of the prismatic layer, cause the crumbling away of this rather brittle material. If the oyster cannot keep pace with this process, it will be unable to enlarge its flat valve, as it lacks the support on which it should deposit its harder calcareous layers. It

seems possible that the flat valves of LÉLOUP's oysters not only failed to grow, but even decreased in diameter. As the scales crumble away or offer insufficient shelter because of overcrowding, *Polydora* may start to dig into the calcareous layers in an effort to obtain more shelter. If *Polydora* abounds as it did in the Bassin de Chasse, even the calcareous layers of the oyster's flat valves may crumble away eventually. LÉLOUP's data are not sufficient to estimate to what extent this occurred at Ostend.

I am inclined to assume that a steadily decreasing diameter of the oyster's flat valve will more readily induce the oyster to curl up the edge of its cupped valve in an effort to make both shells meet normally, than just a lack of growth of the flat valve. I am not so sure that the new position of the oyster's shell aperture (facing upwards), in combination with the deposition of silt and debris by *Polydora*, was the direct cause of the death of LÉLOUP's oysters.

Peculiarly enough, *Polydora ciliata* is not always satisfied with making its long mud-burrows between the scales of the oyster's flat valve. Sometimes it starts digging into the calcareous parts of the oyster's shell, especially in the cupped valve. SÖDERSTRÖM (1923) made it clear how *Polydora* manages to do so. It may start living in a tube parallel to the shell's surface, and later begin to dig in it, in which both a secretion of some acid or other and a mechanical burrowing executed by strong stout bristles are said to participate. *Polydora* then creates a U-shaped burrow of which the part facing the surrounding seawater may be lengthened by shorter or longer cylindrical mud-tubes, protruding from the shell or from any other type of supports it lives in (e.g. limestone, peat-soil). *Polydora*'s occurrence in such different types of substratum indicates that it burrows primarily for shelter, and has no parasitical relations with the living oyster. At most it can be considered as one of the oyster's competitors for food.

Others have noted this difference in the worm's behaviour before, but there is insufficient evidence to support FERRONNIÈRE's (1901) and SCHODDUYN's (1931) suggestions that there are two or more distinct races of *Polydora ciliata*, each with a different way of living. In fact all possible transitions may be found. Those living innocently in their mud-burrows between the scales of the oyster's flat valve may some day or other start taking calcareous shell material away to deepen their burrow, and eventually may create a perfect U-shaped burrow, communicating with the outer world through the usual soft lengthening tubes. In digging a burrow, *Polydora* makes but one hole, broader than wide, in which a separating wall is constructed out of debris to obtain the required U-shape (SÖDERSTRÖM 1923, LAMY & ANDRÉ 1937). Little

is known about the factors which may induce *Polydora ciliata* to leave its mud-burrows and to create a burrow in hard calcareous material. I explained above that a shortage of suitable shelter among the scales of the oyster's flat valve, caused by overcrowding or by the gradual crumbling away of the scales, may force *Polydora* to dig into the calcareous matter in search for a more adequate shelter. The same may hold good for those larvae of *Polydora ciliata* which have not succeeded in finding an easy place to make a mud-burrow, and have finally settled on some hard and smooth material, like the cupped valve of an oyster, where only burrowing can offer adequate protection. It certainly would be interesting to study the factors influencing its way of living in greater detail. The behaviour of *Polydora* larvae should be included in such a study.

Trouble may start when *Polydora* digs so deep in the shell of a living oyster, that it threatens to perforate the latter's shell. The mechanical irritation, the secretion of acid, the possible excretion of some toxic organic product, and the contact with the mud-deposits of *Polydora*-burrows may threaten the oyster's well-being if its shell becomes perforated. A healthy oyster is able to make a seal of olive-green conchyolin, exactly in the place where the *Polydora* burrow threatens to perforate the shell. In due course normal calcareous layers can be deposited on the conchyolin seal. The oyster can produce either pure conchyolin or normal calcareous shell layers, as circumstances demand. As conchyolin cannot be dissolved by *Polydora*'s acids, such a sealing off is far more effective than the deposition of only a thin layer of calcite. I presume that the elastic conchyolin also resists for quite a while the mechanical action of *Polydora*'s bristles. When the perforations of the shell are not extremely numerous, and the oyster is not too weak to react promptly to threatening perforations, the oyster does not seem to suffer much from these activities of *Polydora*. Both HOEK (1902) and LAMY & ANDRÉ (1937) claim that too vigorous an attack of drilling *Polydora* may bring about the oyster's death: "Si les *Polydora* sont très nombreux le mollusque finira par mourir de l'excès de travail qui lui est imposé." HOEK's additional statement, that serious danger is involved if *Polydora* perforates the oyster's shell under the muscle, where the oyster is unable to secrete calcareous material, is certainly not based on HOEK's own observations, but has been derived from CARAZZI's descriptions.

I can add that *Polydora ciliata* very often makes its burrows in the shells of oysters in the Zealand waters. A threatening perforation is practically always sealed off promptly by deposition of small circular patches of conchyolin. Only in the case of an exceptional mass-attack

larger green patches of conchyolin are laid down in an effort to avoid a direct contact with the worm.

I could not see that serious damage by *Polydora*'s drilling ever led to a sheer exhaustion of oysters in Dutch waters. It may have been different in HOEK's time (1902) when the Zealand oysterbeds were overpopulated, which resulted in poor growth and a complete lack of growth in mid-summer. Nowadays our oysters never stop depositing shell material from early in May till well into November, so that *Polydora*, active in the warmer season, can be sealed off at any time. Sometimes, however, *Polydora ciliata* may be so numerous, that the honey-combed shells become so brittle that they are easily broken during packing or transportation. Some parts of the Zealand beds are notorious for this (e.g. the Dijkwater).

Quite another type of damage by *Polydora ciliata* in Dutch waters is the above-mentioned loss of oyster larvae through the voracity of *Polydora*. Further *Polydora ciliata* also likes to make its burrows under the lime-coating of the tile-collectors. If crabs (*Carcinides maenas*) find that *Polydora* is particularly numerous there, they may start peeling off the lime-coating in search for *Polydora*, and thus destroy quantities of oyster spat.

The most serious damage to the oyster industry in many parts of the world is imputed in the literature to *Polydora ciliata*. In practically every case presented *Polydora ciliata* could plead not guilty, and point to other members of the *Polydora* family as the culprits. I have not enough space here to clear up the confusion which is found in the literature on this point. It is enough to mention that *Polydora ciliata* most probably does not occur at all in America (HARTMAN 1945), and Australia, from where its harmful effects have been reported.

Polydora hoplura CLAPARÈDE

Much of the havoc caused in many important oyster districts, and ascribed to *Polydora ciliata*, has in fact been caused by *Polydora hoplura* or by biologically closely related species like *Polydora websteri* HARTMAN. The latter species all show the same way of living, differing from that of *Polydora ciliata*.

Polydora hoplura and biologically related species usually do not start their work from the shell's exterior surface, as *Polydora ciliata* does, but penetrate between the oyster's mantle and shell. Very frequently according to my observations this is done opposite the oyster's inhalent chamber, though penetration under the mantle of the exhalent chamber does occur occasionally. *Polydora hoplura* then does not wander at random between the oyster's mantle and shell, but settles down at the edge of the shell and in a direction approximately perpendicular to

this. It soon starts to accumulate mud, as *Polydora ciliata* does after settling down between the scales of the oyster's flat valve.

Both the presence of the worm itself and the accumulation of mud and debris irritate the oyster. The oyster responds with efforts to seal off the intruder, either with conchyolin layers (far larger green patches than the neat round ones used against *Polydora ciliata*) or with harder calcareous layers. If the oyster is not for any reason in too poor a condition, these efforts are successful. The result is favourable for *Polydora*, however: it has got a solid and safe burrow without any burrowing in hard shells. Its communication with the surrounding sea-water is better and safer after the oyster has deposited its calcareous layers: the worm can then reach the outer world at any time without running the risk of being caught by the oyster's tightly closing valves.

The oyster on the other hand, is at a marked disadvantage. An oyster always prefers a smooth interior surface to its shell. To this end it fills in all furrows and possible dimples in its shell with chalky deposits (KORRINGA 1951). Probably a smooth and well-shaped interior surface of the shell promotes the proper functioning of the oyster's intricate filtering mechanism. By covering *Polydora hoplura* and its mud deposits with calcareous layers, it cannot avoid making a more or less serious hump on the shell's interior surface. It is far more difficult to smoothe away a hump than a furrow or dimple in the shell.

If the position of the oyster's shell on the sea-bottom renders it necessary, *Polydora hoplura*, living in its perfectly safe shelter, can lengthen its burrow with a shorter or longer mud-tube. The growing *Polydora* needs a more spacious burrow, and to that end perforates the thin blister the oyster laid down on it. More mud is then deposited. The oyster covers it again, but has to put up with a still larger and higher hump, now reaching further from the shell's edge. This can go on for quite a while until extensive blisters, often filled with black mud, can be found on the shell's interior surface, which thus often becomes seriously uneven. *Polydora* usually perforates the blisters repeatedly at the end away from the shell's edge. The part of the burrow at the edge of the shell becomes covered by thicker and thicker layers of calcareous matter as the shell grows. Finally the exit of the *Polydora* burrow no longer is to be found on the shell's edge, but somewhere on the outside of the valve away from the edge.

The result of this work of *Polydora hoplura* and its biologically allied species differs completely from that of *Polydora ciliata*. The activities of the former lead to burrows built on the shell's interior surface, starting at the shell's edge and perpendicular to that edge. Humps on the shell's interior surface are the result. If the oyster is rather weak only thin layers cover *Polydora* and its mud deposits. In very weak oysters *Polydora*

and its mud patches may be practically bare under the oyster's mantle. *Polydora hoplura* may deepen its burrow by extending into the shell layers underneath itself. Just as with *P. ciliata*, it usually lives in a U-shaped burrow with the legs of the U very close together. The separating wall has been built of debris. Sometimes, however, the worm deviates more or less from this scheme, makes a curve in its burrow somewhere away from the edge, or makes an open U instead of keeping the legs close together.

An oyster shell seriously attacked by *Polydora ciliata*, on the other hand, shows burrows of more modest dimensions (about $\frac{1}{2}$ to $\frac{1}{3}$ as wide as those of *P. hoplura*) which strike the interior surface of the shell at all possible angles and in all possible places. There is no relation to the shell's edges. Only the distal ends of the burrows threaten to perforate the shell.

Unless the oyster is too weak to seal off *Polydora hoplura*, which may be the case in mid-summer in southern countries and in overpopulated districts, a few *Polydora* do not endanger the oyster's life. In districts rich of food even a mass attack in which younger blisters of *Polydora* may be produced on top of the older ones does not necessarily affect the oyster's well being for the oyster can lay down as much shell material at any time as it requires without becoming exhausted (c.f. LOOSANOFF & ENGLE 1943).

Though it is fairly easy to tell the work of *Polydora hoplura* and biologically closely related species from that of the more innocent *P. ciliata*, there exists a terrible confusion in the literature. As early as 1736 DESLANDES described the "red worms" in the oysters shells and believed they had some share in the oyster's fertilization ("vers accoucheurs"). He advised the oystermen to lay out blocks of limestone to divert *Polydora*'s attention from the oysters.

GIARD (1881) gave the same advice as he saw the burrows of *Polydora ciliata* abounding in limestone rocks near Dieppe. Unless one kills the *Polydora* in such limestone blocks at frequent intervals, I assume that such measures could only promote the occurrence of the worm. Moreover GIARD knew very well, that it is *Polydora hoplura* (*Leucodora sanguinea*) which does the real damage in the French oyster districts, and I never heard that this species likes to dig its burrows in limestone rocks, as *Polydora ciliata* does.

CARAZZI (1893), though giving much valuable information on *Polydora* and its activities, erroneously ascribed mud-blisters caused by worms entering between the oyster's shell and mantle to *Polydora ciliata*, which added to the confusion. MCINTOSH (1902) had never seen the activities of *Polydora hoplura*, and concluded from his own experience

with *Polydora ciliata*: "The perforations of *Polydora* in oysters need not be taken too seriously since even the best oysters are thus invaded and yet, their quality is undisputed." McINTOSH discussed and criticised HASWELL (1885) and WHITELEGGE's (1890) reports on the havoc caused by *Polydora* in Australia's oyster district, which they erroneously ascribed to *Polydora ciliata*. No doubt it had been caused by *Polydora hoplura* or by some species with the same way of living as the latter.

Polydora hoplura does not belong to the regular fauna of Dutch waters. It has never been found on my experimental oysters at Yerseke. It has, however, repeatedly been imported with Brittany oysters. For the first time since I started my investigations in the Oosterschelde (1937), I noted in the year 1949 that specimens of *P. hoplura* introduced thus did reproduce successfully in Dutch waters. Several Dutch oysters in the autumn of 1949 showed a blister caused by *Polydora hoplura*. This gives cause for anxiety. We hope that *Polydora hoplura* will disappear again from the Dutch waters and that its reproduction in 1949 may be ascribed to the prolonged warm weather in that particular year. If it should increase in numbers, we must be ready to combat it efficiently. We know already that it is fairly easy to kill the worm in its blister without affecting the oyster, at least while the latter is still strong and healthy. A bath in a dilute solution of poison may be used to that end.¹

Polydora hoplura, which has considerably larger eggs than *P. ciliata*, is said to have a far shorter pelagic life than the latter. I even wonder whether it may reproduce occasionally without any intermediate pelagic life at all, for many relaid French oysters showed far higher numbers of *Polydora* blisters in the part of their shell laid down during the sojourn in the Oosterschelde than Dutch oysters of the same size and from the same beds. Or do adult worms occasionally leave their burrow to make a new start at some other point of the same shell? Is it of any advantage to *Polydora* to try to keep the entrance of its burrow somewhere close to the edge of the oyster's shell? Does it take any advantage of the water current created by the oyster during feeding hours? How long is the life of an average *Polydora*? During a cold spell in January 1950 most of the *Polydora hoplura* born in 1949 disappeared. Those kept in a covered oyster basin with controlled water temperature survived however. More questions could be put. Therefore, for this

¹ In the year 1950 both *Polydora hoplura* and *P. ciliata* became so numerous in the Oosterschelde that we had to advise the oysterman to control these pests. The application of fresh water for 16 hours or a 3-hour bath in a $\frac{1}{2}\%$ solution of D.N.C. (di-nitro-ortho-cresol) suffices to kill both *Polydora*'s quantitatively without affecting the oyster (KORRINGA, P., *Polydora als vijand van de oestercultuur*. Visserij-nieuws 3, no. 10, supplement, 12 p.).

species of *Polydora* too, a more detailed investigation on its way of living would be more than welcome to both the pure and the applied biological science.

Cirratulidae:

Cirratulus cirratus (O. F. MÜLLER).

Up till now few specimens of this worm have been recorded from the Dutch coast. The Leyden Museum possesses undated specimens from Den Helder and from Walcheren. Possibly the latter are those collected by HORST at Veere (c.f. HORST 1919. Tijdschr. Ned. Dierk. Ver. p. 25).

Is it possible that it has not been looked for in the right habitat? FAUVEL (1927) states that it lives in mud deposits in crevices of rocks or in the muddy sand under stones. Though I took bottom samples in many places in the Oosterschelde, I only came across one specimen of *Cirratulus cirratus* in a sample rich in shell debris from plot 446 (29-4-1941).

I did find several specimens, however, on oyster shells, but invariably on those taken from the plots, and never on oysters kept in a tray. This confirms THORSON's view (1946) that *Cirratulus cirratus* does not possess pelagic larvae. It therefore cannot easily reach oysters in a tray. The following specimens have been collected by me:

p. 417.	21-10-1940	2 on 10 oysters
p. 338.	24-10-1940	1 on 10 oysters
p. 408.	24-10-1940	1 on 10 oysters
p. 417.	8- 5-1941	10 on 10 oysters
p. 339.	7-10-1940	1 on 25 one-year-old oysters
p. 37c Grevelingen	April 1941	1 on 10 oysters

Cirratulus was invariably found between the scales of the oyster's flat valve, where it found small quantities of a sandy mud. I can hardly believe that this could be its only habitat. It indicates that crevices do appeal to *Cirratulus*, as FAUVEL stated, and that this species avoids extensive deposits of sand, mud and peat. Perhaps we shall find it later in greater numbers.

Tharyx multibranchiis (GRUBE).

This species, closely related to *Cirratulus*, has distinct eyes, one pair of palps, and a great number of long cirriform branchiae. One wonders how it manages to prevent them getting knotted up. It has never been recorded from Dutch coastal waters. It appeared to be fairly common in the Oosterschelde, for I found it in many bottom samples, though only once in great numbers:

p. 188 bottom sample.	3-12-1940	10 specimens (about 10 mm long)
p. 443 mud and peat	3-12-1940	4 specimens
p. 551 bottom sample.	16-12-1940	1 specimen
Tidal basin Vendeville, Yerseke	20-11-1940	2 specimens
p. 157 bottom sample rich in shell debris	16- 5-1941	30 specimens
p. 448 bottom sample rich in shell debris	29- 4-1941	12 specimens
p. 486 bottom sample.	27- 4-1941	2 specimens
Katsche Gat, Zandkreek, mud .	18-11-1940	7 specimens

Moreover I found it twice on the shell of a living oyster, where it no doubt did arrive accidentally as a youngster:

p. 491	25- 4-1941	1 on 10 oysters
„Kijk-uit”, Yerseke.	25- 8-1941	1 specimen on 50 oysters born in 1939

Both specimens recorded here have been found between the scales of the oyster's flat valve.

Dodecaceria concharum ØRSTED.

Though recorded before from the Dutch coast, *Dodecaceria concharum* seems to be rather rare here. The Leyden Museum possesses material collected on the oyster beds of the Oosterschelde by HOEK (1901). It can make its burrow in old shells, but does not seem to be able to drill holes in hard healthy shell material or in hard lime stone.

MOEBIUS (1893) found it on the German natural oyster beds and stated: “*Dodecaceria* sitzt in den Schalen älterer Austern in kurzen unregelmässig gebogenen Röhren.” SCHODDUYN (1931) found 2 specimens on an English oyster. LAMY & ANDRÉ (1937) state that it occurs from Norway to Madeira, and makes its elliptical U-shaped burrows in soft lime-stone and old shells, especially in those of *Ostrea*, *Cyprina* and *Pecten*.

I found one small specimen in an old oyster shell in the oyster basin at Bergen op Zoom (29-11-1940), and later 15 more specimens on an old oyster taken from plot 524 (4-4-1941). Most of these specimens were found to have constructed their burrow between the shell of the oyster and its collector (an old decayed shell of *Tapes*); some lived between the scales of the oyster's flat valve. Apparently the *Dodecaceria* on this oyster had not gone to any trouble to drill burrows in the more resistant parts of the oyster's shell.

Streblospio Dekhuyzeni HORST. (fig. 12).

This species, hardly differing from *S. Shrubsolei* (BUCHANAN), was common in the former Zuiderzee (HORST 1922). DE VOS (1936) even

said it was the commonest Polychaete in the Zuiderzee in the period 1927-1932. As it did not occur in the Northern part of the Zuiderzee, she added that this species is characteristic of brackish water, and cannot stand high salinities.

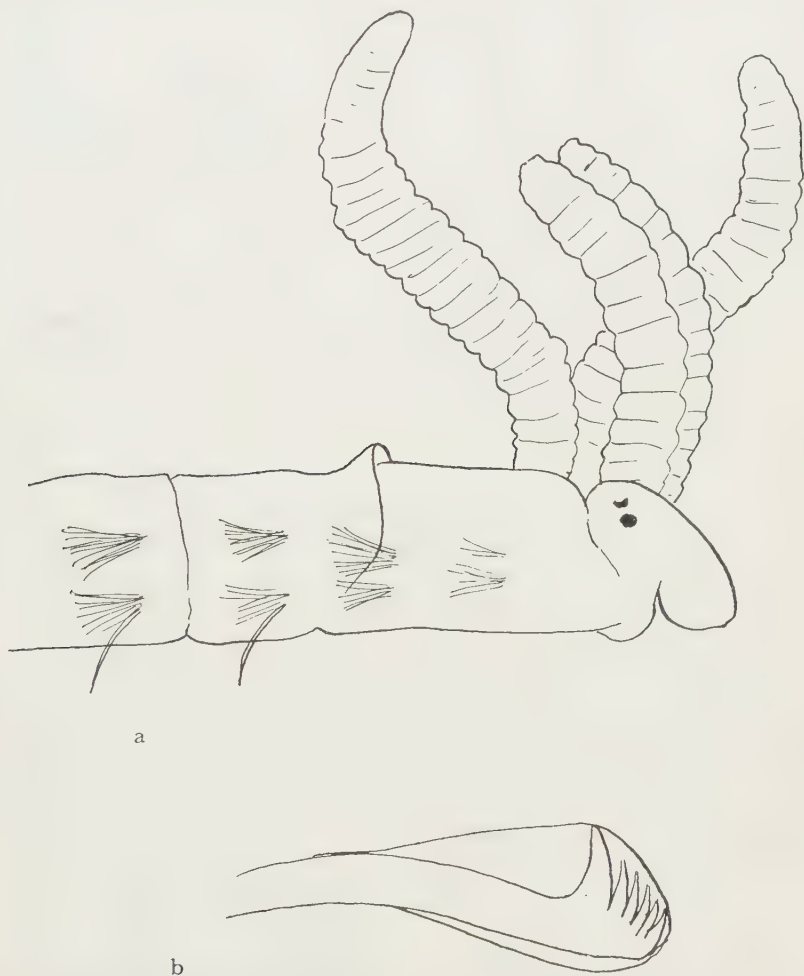


Fig. 12. *Streblospio Dekhuyzeni* HORST; a. anterior end, side view; b. hook, 9th setigerous segment

I cannot corroborate this view, for I found *Streblospio* in 2 stations in the Oosterschelde, where the salinity is fairly high and constant (28‰):

Katsche Gat, Zandkreek in mud	18-11-1940	1 specimen
Tidal basin Vendevele, Yerseke		
in mud	20-11-1940	4 specimens

LELOUP (1940) found it in the Bassin de Chasse at Ostend, where the water was likewise of a high salinity.

Capitellidae:

Heteromastus filiformis (CLAPARÈDE).

This species is very common in sediments rich in mud. In his treatise on the Polychaete worms of the Zuiderzee HORST (1922) identified it wrongly as *Capitella capitata*. DE VOS (1936) rectified this error, and stated that *Heteromastus* certainly was very common in the former Zuiderzee. LELOUP found it at Ostend in the Bassin de Chasse.

I found it in practically every bottom sample I took in the Oosterschelde, which indicates its wide distribution there:

Katsche Gat, Zandkreek . . .	18-11-1940	4 specimens
Kattendijke	21-11-1940	8 specimens
Tidal basin "Kijk-uit", Yerseke	20-11-1940	2 specimens
Tidal flats "Kijk-uit", Yerseke	20-11-1940	7 specimens
Tidal basin Vendeville, Yerseke	20-11-1940	9 specimens
p. 446 bottom sample.	29- 4-1941	2 specimens
p. 184 mud	20- 6-1941	3 specimens
p. 448 mud	29- 4-1941	2 specimens
p. 188 sandy mud	3-12-1940	15 specimens
p. 443 sandy mud	3-12-1940	10 specimens
p. 551 sandy mud	16-12-1940	1 specimen

I never found it on the shells of living oysters.

Capitella capitata (FABRICIUS).

Withdrawing HORST's (1922) erroneous Zuiderzee records, only some Dutch specimens of *Capitella capitata*, collected in recent years, are to be found in the collections of the Leyden Museum.

On several occasions I collected *Capitella capitata* in the Oosterschelde. This often blood-red worm has been found there in bottom samples, especially in those rich in shell debris:

Tidal basin "Kijk-uit", Yerseke	6-11-1940	15 specimens
Tidal flats "Kijk-uit", Yerseke	20-11-1940	9 specimens
Tidal basin Vendeville, Yerseke	20-11-1940	5 specimens
Katsche Gat, Zandkreek . . .	18-11-1940	1 specimen
p. 446 bottom sample.	29- 4-1941	2 specimens
p. 184 bottom sample.	20- 6-1941	4 specimen

Occasionally I found one on an oyster, hidden between the scales of the flat valve:

Year	Oysters born in	Period
1941	1939	20/5 (1), 25/6 (2), 17/7 (1)
1942	1940	22/6 (1 juv.)

Most probably their occurrence here is purely accidental.

I moreover found some specimens in the boxes with wire gauze, placed at Yerseke in the year 1940 (table III).

It should be recorded here that *Capitella capitata*'s characteristic features are liable to some variation. Though according to FAUVEL (1927), and HARTMAN (1945) the first 6 thoracic segments should bear pointed setae only, and no hooks, I sometimes found hooded hooks on the 6th segment too. Especially small individuals may show less than 6 segments with pointed setae only. In one and the same individual left and right side may differ in this respect. The shafts of the hooded hooks are sometimes distinctly inflated. The pointed setae are sometimes seamed on both sides, though always broader on the convex side. The genital hooks vary in number. Uneven numbers may occur. I once found a male individual with 4 pairs of heavy hooks anterior to and 2 pairs posterior to the genital aperture. In this specimen too, a number of smaller hooks could be found at the bases of the long ones.

Arenicolidae:

Arenicola marina (L.) (fig. 13).

On oysters taken from a tray placed on plot 551, I found (21-10-1940) 2 specimens of a small Polychaete worm, which measured 5 to 6 mm, and was difficult to identify. Making use of FAUVEL's keys (1927), I invariably landed in the family of the Maldanidae, but I could not find one description of a Maldanid species which matched my specimens.

It is a worm of approximately cylindrical shape. The posterior part, more slender than the rest of the body, consists of non-setigerous segments. The head, bearing 4 eyes, is followed by some non-setigerous segments, indistinctly separated from the head. Next follow 19 setigerous segments. These setigerous segments bear at their dorsal sides pointed setae only at their ventral sides hooks. As a rule each dorsal ramus has but one long and slender seta, seamed on both sides, and one shorter spatulate seta, likewise seamed on both sides. The latter setae are ciliated at one side. The hooks are crowned with several teeth, of which one or two predominate. The shafts of the hooks are curved and inflated. At both sides the number of hooks per segment rises from the first setigerous segment (2 hooks) to the last (7 hooks), which hooks are all placed in one single row. The worms are red, and live in a tube made of fine sand particles bound together with a sticky slime. Head and pygidium bear yellow pigment spots.

I sent one of my specimens to Prof. FAUVEL for identification. It took a very long time in the years of the German occupation, for such a parcel to reach its destination in another country. Meanwhile I had

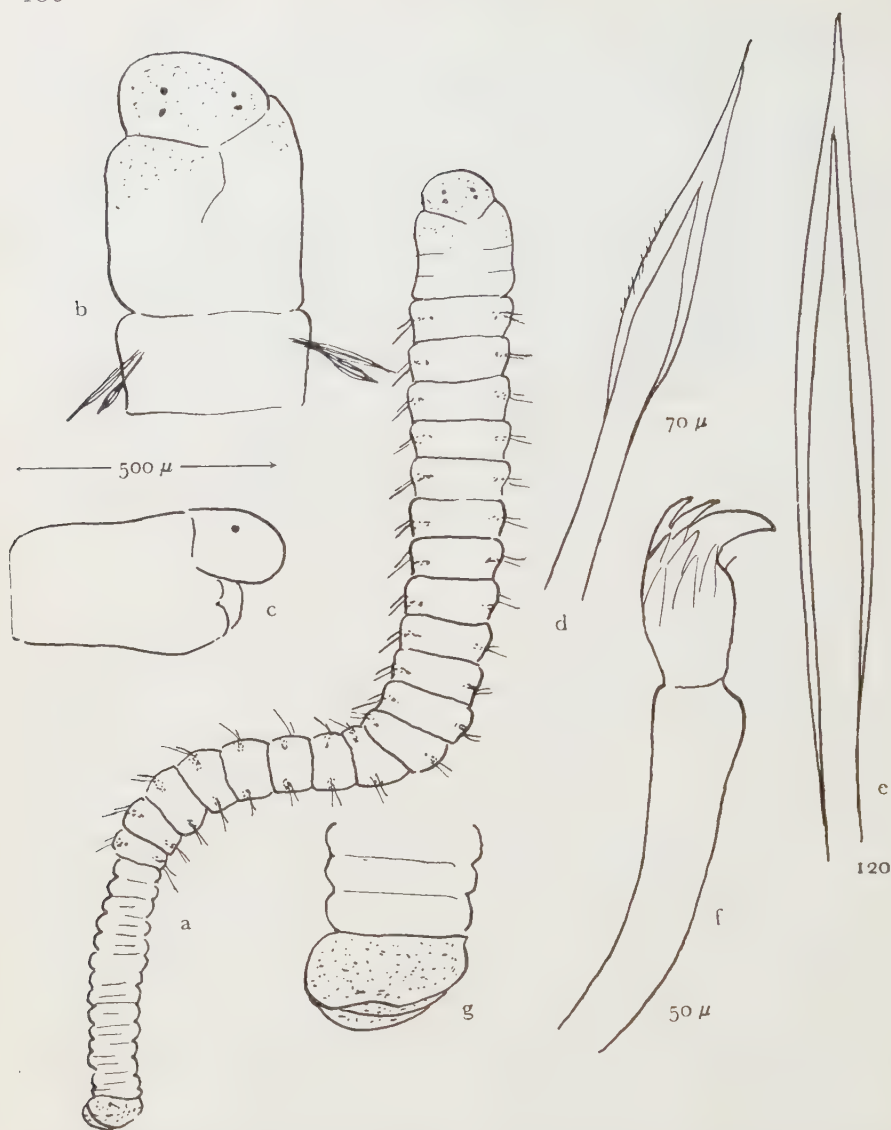


Fig. 13. *Clymenides*-larva *Arenicola marina* (L.). a. entire animal 5 à 6 mm; b. head, dorsal view; c. head, side view; d,e. neuroseta; f. hook; g. pygidium

found a larger specimen, measuring slightly over 10 mm, which showed the following additional features: short proboscis bearing many papillae; 2 otocysts containing several otoliths; 2 distinct oesophageal coeca; short non-ramified cirriform branchiae, set close to the setae, and connected with the vascular system; an increasing number of

pointed setae per segment. I figured then that it might be a young specimen of *Arenicola marina*. Then, Prof. FAUVEL's answer came, informing me that it was *Clymenides ecaudata*, the larva of *Arenicola marina*. Others too had experienced difficulties in its identification. It was FAUVEL himself who finally demonstrated that *Clymenides* is nothing but the larva of *Arenicola*: "MESNIL en avait fait jadis le type d'une famille nouvelle, les Arenicolo-Maldaniens, avant que j'aie démontré qu'il s'agissait tout simplement de stades jeunes d'*Arenicola*" (FAUVEL 1941, in litt.).

I found the following specimens of the *Clymenides* larva of *Arenicola* on my experimental oysters:

Year	Oysters born in	Period
1941	1940	30/5 (1), 17/7 (1)
1941	1939	25/6 (1), 4/7 (5), 10/7 (2), 31/7 (2), 22/9 (1)
1942	1941	9/6-14/7 few but regularly
1942	1940	22/6 (2)
1943	1942	2/6-20/7 few but regularly
1943	1941	15/6 (2), 14/7 (3)
1944	1943	22/6 (2), 28/6 (1), 19/7 (1)

On other oysters kept in trays I found:

"Kijk-uit", Yerseke.	6-11-1940	2 specimens
p. 551	8- 5-1941	2 specimens

On oysters taken from the plots I found:

p. 835 Ouwerkerk	24- 4-1941	1 specimen
p. 417	8- 5-1941	2 specimens on 10 oysters

Moreover I once encountered a *Clymenides* in a plankton sample (19-6-1942). It does not seem to be a good swimmer. Possibly it had been whirled up by the currents, like so may other benthonic organisms I found in my plankton samples which are taken 2 feet from the bottom only.

The tabulation above proves that *Clymenides* larvae may be found at least from April to November. Most of my specimens were collected in June and July. I do not claim that the shell of the oyster is the only habitat of *Clymenides*. Far more of them must live in other places, somewhere in the Oosterschelde. I never found it in my bottom samples, but possibly it prefers a very special habitat, not covered by my sampling.

Though *Arenicola marina* is very common creature in our waters, we

do not know very much about it. THORSON (1946) and NEWELL (1948) agree that *Arenicola* breeds in October or thereabout in our latitude. Spawning is most probably concentrated within a very few days only, presumably an example of lunar periodicity (c.f. KORRINGA 1947) requiring closer investigations. Not much is known about what happens next. THORSON (1946) never found planktonic larvae, and assumes that *Arenicola* does not produce them. Very young bottom stages could be found late in autumn. THORSON assumes that they grow fairly slowly, and become distinct little *Arenicola* in the next summer season. NEWELL (1948) found the young larvae, 14 days old, measuring 0.25 mm, in the silt high up in the *Fucus*-zone, far away from the spawning adults. NEWELL too, claims that *Arenicola* has no extended pelagic larval phase. NEWELL lost sight of the larvae until he found young worms 10 to 20 mm long, and typical little *Arenicola*, in the following spring. In September those appeared to have already reached a length of over 40 mm. Considering the difference in habitat of larval, young, and adult *Arenicola*, NEWELL assumes that "lugworms sometimes leave their burrow and swim for short distances, probably to seek situations for new burrows. This kind of migration may be responsible for dispersing the animals throughout the habitat and accounts for its repopulation by young worms from the edge of the *Fucus* zone." The latter assumption is supported by observations of an occasional swimming *Arenicola*.

What can I add to this? In the first place, that I encountered an occasional swimming *Arenicola* myself, while wading on the oyster grounds. Sometimes, however, *Arenicola* must swarm in tremendous numbers. In the early spring of 1949 I investigated a sample of spent herring caught by a Bergen op Zoom fishermen in his fish-weir. Their stomachs appeared to be crammed with *Arenicola* of medium and fair size, most unusual for a plankton eater like the herring. As every herring of the sample was chock-full of *Arenicola*, the latter must have been swimming around in fair numbers, for nobody would claim that herring dig the lugworms out of their burrows.

As to the development of the larvae, I feel that both THORSON and NEWELL overestimated their growth rate. As I found *Clymenides*-larvae throughout the summer season, it evidently is a slow grower. I assume that the larvae born in October will spend the whole of the next summer as a *Clymenides*. Only when about a year old does it gradually change into a typical little *Arenicola*. Those found in spring in the Whitstable area (NEWELL 1948), which measured 10 to 20 mm and showed all the features typical for *Arenicola*, cannot possibly belong to the same generation as the tiny 14-days larvae NEWELL found a few months earlier. According to me, NEWELL and THORSON both overlooked the extended *Clymenides* phase in the development of *Arenicola*.

FERRONIÈRES (1901) found the *Clymenides* larvae, in the oyster parks at Le Croisic.

From my data I am inclined to conclude that the tiny benthonic larvae of *Arenicola* born in October, develop into *Clymenides* larvae in due course. The latter metamorphose into a complete *Arenicola* at the age of about one year. The young *Arenicola* found by NEWELL in April probably are about 18 months old.

Clymenides larvae must occur in great numbers in many districts. Those to be found on the shells of oysters probably belong to a minority, which settled accidentally in that habitat. For, *Arenicola* may abound where oysters are lacking. Moreover, even if one *Clymenides* should occur on every 10 oysters, their number would still be insignificant for a regular recruitment of the vast stock of *Arenicola* in the Oosterschelde.

Once we know where to look for *Clymenides*, we shall find them. They are inconspicuous, because they usually hide in a narrow tube, made out of a sticky slime and small sand grains. Though *Clymenides* is a very muscular little worm, and occasionally gets whirled up in the plankton, I still wonder how they reached my oysters in the trays.

Sabellariidae:

Sabellaria spinulosa LEUCKART.

In several oyster districts *Sabellaria* gives cause for anxiety, since it grows in such tremendous numbers on the oysters that the latter may be suffocated. MOEBIUS (1893) found here and there practically every oyster he caught covered with the hard sand tubes of *Sabellaria*. The French oystermen too know how much trouble the "hermelles" can give. DOLLFUS (1921) mentions in this respect the beds of Cancale and Mont St. Michel as notorious *Sabellaria* districts.

I do not know why *Sabellaria* does not bother the Dutch oyster industry. Can it be that winter temperatures in the Oosterschelde, though differing little from those prevailing in the beds MOEBIUS investigated, are too low for this species? Or does *Sabellaria* require a salinity higher than 28 ‰ (Oosterschelde average) to breed and develop normally? Occasionally *Sabellaria spinulosa* has been introduced alive with oysters from Arcachon, e.g. in April 1947. On October 6th, 1947, I found living *Sabellaria* full of spawn on such relaid Arcachon oysters. Purple drops containing many eggs exuded from the *Sabellaria* burrows but I did not find their offspring, though the 1947/48 winter was a mild one.

Only once did I find the hard sand burrow of *Sabellaria* on a Dutch oyster viz. 13-12-1938. This oyster came from one of my trays, placed on plot 387. Spat, newly detached from the tile-collectors, had been put

in that tray in the spring of 1938. I am therefore sure that this *Sabellaria* settled on a Dutch oyster in the summer of 1938. In the spring of 1938 oysters from Brittany and Archachon had been relaid in fair numbers. I found another Dutch specimen on a tile-collector, February 1950.

Amphictenidae:

Pectinaria Koreni MALMGREN.

For the sake of completeness I record that one juvenile specimen of this species, common on the Dutch coast, was found on my experimental oysters: 25-6-1941, on oysters born in 1939. It apparently does not like that habitat.

Amphitrite Johnstonei MALMGREN.

This sedentary Polychaete worm is not rare on the Dutch coast. HORST (1896) knew of several specimens collected near den Helder. The Leyden Museum possesses specimens from the Waddenzee and from the Zealand waters. MOEBIUS (1893) records several specimens from the natural oyster beds he investigated.

Occasionally I found *Amphitrite Johnstonei* on my experimental oysters:

Year	Oysters born in	Period
1941	1940	30/5 (1 juv.), 17/7 (1)
1942	1941	30/6 (1 juv.)
1942	1940	22/6 (1), 28/7 (2 juv.)
1943	1942	5/7 (1)
1945	1944	5/6 (1)

The specimens collected were all very young. None have been found in my other series.

I also found it on large oysters taken from the plots:

p. 417 8-5-1941 2 on 10 oysters

and several large specimens were got among empty shells in the Bergen op Zoom oyster basin.

My data suggest that *Amphitrite Johnstonei* reproduces in early summer.

Lanice conchilega (PALLAS).

Lanice abounds in the Dutch waters (HORST 1896). Often tremendous numbers of its tubes are cast ashore. MOEBIUS (1893) mentions its occurrence on the German natural oyster beds.

It has been found in fair numbers in the tidal basin I used in the station "Kijk-uit", Yerseke. Its tubes can be detected among the shell debris and stones which cover most of the bottom of that basin. It sometimes settles on oyster shells, e.g. on my experimental oysters:

Year	Oysters born in	Period
1942	1941	25/8 (1), 29/9 (1), 5/10 (1)
1943	1942	14/7 (1), 20/7 (1), 30/8 (1)
1943	1941	8/6 (1), 15/6 (1 juv.), 21/6 (1 juv.)

And none in my other series.

I also found it on oysters taken from the plots:

p. 143 22-7-1941 2 on 15 oysters

It often occurs in fair numbers in the trays the oystermen place off Yerseke:

tray p. 261 23-7-1941 8 on 25 oysters

THORSON (1946) states that *Lanice* larvae abound in the summer plankton of the Kattegat. I often found it in my plankton samples too. This little creature lives in a hyaline tube, the shape of a truncated cone, which seems to be far too wide for it. I recorded their occurrence in plankton samples on 27-6-1941, 19-6-1942, 24-6-1943, but saw them many more times. It apparently breeds in summer.

Serpulidae:

Spirorbis Pagenstecheri QUATREFAGES.

The little spiral shaped tubes of *Spirorbis* are often found on stones and shells collected on the oyster beds, especially on the intertidal flats. For a proper identification, living material, complete with operculum, is to be preferred.

I found 2 specimens which turned out to be *S. Pagenstecheri* on oysters in a tidal basin near the harbour of Yerseke (26-11-1941), and 2 more specimens of *S. Pagenstecheri* on my experimental oysters: 6-9-1943, on oysters born in 1941.

OLIGOCHAETA

Peloscolex benedeni (UDEKEM).

DE VOS & REDEKE (1941) recorded *Peloscolex benedeni* for the first time from the Dutch coast and stated that it abounded in bottom samples

taken on the tidal flats in the Province of Groningen. Specimens collected by LELOUP (1940) in the Ostend Bassin de Chasse, were identified as *Peloscolex benedeni* by miss DE Vos. I found it in many bottom samples taken in the Oosterschelde. The specimens collected were identified by Miss DE Vos:

Tidal basin "Kijk-uit", Yerseke	6-11-1940	25 specimens
Tidal flats "Kijk-uit", Yerseke	20-11-1940	3 specimens
Tidal basin Vendeville, Yerseke	20-11-1940	30 specimens
Katsche Gat, Zandkreek, mud.	18-11-1940	26 specimens
p. 551 bottom sample.	16-12-1940	2 specimens
p. 188 bottom sample.	3-12-1940	15 specimens
p. 157 bottom sample.	16- 5-1941	4 specimens
p. 184 bottom sample.	20- 6-1941	5 specimens
p. 446 bottom sample.	29- 4-1941	3 specimens

These data indicate that *Peloscolex benedeni* is probably of very common occurrence in the Oosterschelde.

I also found it on the shells of oysters, but only once on an oyster kept in a tray in my regular series:

21-6-1943 1 specimen on 25 oysters born in 1941

On oysters taken from the plots the following specimens have been collected:

p. 491 25-4-1941 3 on 10 oysters
p. 835 Ouwkerk 24-4-1941 1 on 10 oysters

Paranaïs litoralis (ØRSTED).

This Oligochaete worm, recorded by DE Vos on several occasions from Dutch coastal waters and from Ostend (LELOUP 1946), has been found in several of my bottom samples, and sometimes on shells of oysters. Miss DE Vos identified my specimens:

Katsche Gat, Zandkreek . . .	18-11-1940	7 specimens
Tidal basin Vendeville, Yerseke	20-11-1940	20 specimens
Tidal flats „Kijk-uit”, Yerseke.	20-11-1940	4 specimens
p. 443 bottom sample.	3-12-1940	2 specimens

On shells of living oysters have been found the following specimens:

Year	Oysters born in	Period
1941	1939	20/5 70 specimens
		16/6 18 specimens
		10/7 1 specimen
1942	1940	9/6 2 specimens
		16/6 3 specimens
1943	1941	8/6 2 specimens
1944	1943	22/6 1 specimen

Moreover on oysters kept on trays in the Bergen op Zoom oyster-basin:

22-7-1942.	2 on 25 oysters
5-8-1942.	4 on 25 oysters

As practically all the specimens from my regular series were collected on the 2-year old oysters, and that shortly after the trays had been placed in the station 'Kijk-uit', Yerseke, I presume that *Paranaïs* settled on the oysters in the basin at Bergen op Zoom in which those oysters hibernated. The occurrence of *Paranaïs* on oysters living in the Bergen op Zoom basin in mid-summer, and their absence on oysters from the plots, on oysters from trays placed in different stations, and on oysters of my regular series sampled later in the season, support my view that it is the Bergen op Zoom oyster basin which obviously offers favourable conditions to *Paranaïs litoralis*.

PHYLUM ARTHROPODA

CRUSTACEA

OSTRACODA

On several occasions I found Ostracods on the shells of oysters. The late Dr H. C. REDEKE identified my specimens. One species only occurred in fair numbers, and reappeared year after year, so that it should be reckoned among the regular inhabitants of the oyster's shell. This species is:

Loxoconcha impressa (BAIRD)

For my regular series its occurrence can be summarized as follows:

Year	Oysters born in	Period	Maximum
1941	1940	late in September and in October	21/10 24 on 50 oysters
1941	1939	flourishes in October	21/10 90 on 50 oysters 1 per oyster
1942	1941	September/October	
1942	1940	increase mid-September	
1943	1942	fair numbers 30/8-6/10	
1943	1941	some September/October	
1944	1943	few only; no sampling at Yerseke in September and October because of war conditions	
1945	1944	few only	

Moreover I found some specimens on oysters in the Bergen op Zoom basin: 22-7-1942 and 5-8-1942.

Further I found a great number in a bottom sample taken 9-12-1940 in the tidal basin at Yerseke, in which I kept my oysters.

Loxococoncha impressa appeared to occur sporadically in summer, but flourished noticeably in September and October.

Other species of Ostracods have been found on oysters, but only sporadically. It was moreover very difficult to collect these tiny little creatures quantitatively. The following species have been collected on my experimental oysters at Yerseke:

<i>Leptocythere castanea</i> G. O. SARS	Yerseke 11-7-1941
<i>Cythere albomaculata</i> BAIRD	Yerseke 8-7-1942
<i>Cythere viridis</i> O. F. M.	Yerseke 22-6-1942
<i>Cytherura nigrescens</i> (BAIRD)	Yerseke 22-6-1942, 15-7-1942
<i>Cytherois fischeri</i> G. O. SARS	Yerseke 29-9-1942

I did not include these species in the tables, because several specimens must have escaped my attention in other years, and because these little creatures, occurring on my oysters only exceptionally, no doubt exert a negligible influence in the biocoenosis discussed.

On oysters from another station a small number of the species *Hemicythere villosa* G. O. SARS (p. 524, 4-4-1941) have been found.

COPEPODA HARPACTICIDA

A fair number of small Copepods, belonging to the Harpacticids, appeared to occur on the shells of oysters. Especially in the first years of my investigations, I tried to make quantitative collections of these small creatures too. Miss A. P. C. DE Vos studied my material, and published her results in this journal (DE Vos, 1945). One species only:

Longipedia minor Scott

appeared to belong to the regular inhabitants of the shell of the oysters in the station "Kijk-uit", Yerseke. In later years I made only a rough estimation of the number of *Longipedia* occurring on my oysters:

Year	Oysters born in	Period
1941	1940	few until mid-August, fair numbers in September fair numbers in September and October decreases in first part of summer season, flourishes in October
1941	1939	
1942	1941	
1942	1940	few only, very few in September
1943	1942	few, throughout the season
1943	1941	few, throughout the season
1944	1943	some in July, few in August
1945	1944	few only

Longipedia minor abounded on oysters taken from the Bergen op Zoom basin on 22-7-1942 and 5-8-1942.

I did not include in the tables the other species of Harpacticids found on my oysters for the following reasons:

1. They occurred in very modest numbers only, and therefore can hardly have a noticeable influence on the community investigated.
2. In the years 1941 and 1942 only I tried to make quantitative collections of Harpacticids, and even then my figures are not as exact as those of the larger animals collected.
3. A very comprehensive list of the specimens collected in the years 1941 and 1942 has been given by DE Vos (1945).

The following Harpacticids species have been encountered on my oysters:

Longipedia minor SCOTT (c.f. tabulation above) observed flourishing in autumn

Canuella furcigera SARS

Ectinosoma gothiceps GIESBR.

Ectinosoma melaniceps BOECK especially in October

Harpacticus obscurus T. SCOTT

Altheutha interrupta (GOODSIR) large numbers on oysters from a tray, station Harden Hoek, Yerseke 12-8-1941

Parategastes sphaericus (CLAUS)

Tisbe (Idya) furcata (BAIRD)

Dactylopusia latipes BOECK

Dactylopusia micronyx SARS

Parathalestris intermedia GURNEY

Thalestris longimana CLAUS

Diosaccus tenuicornis (CLAUS) autumn species

Amphiascus debilis (GIESBR.)

Amphiascus similis (CLAUS) October

Amphiascus tenellus SARS

Mesochra lilljeborgi BOECK

Mesochra pygmaea (CLAUS)

Nitocra typica BOECK

Ameira parvula CLAUS autumn species

Laophonte curticauda BOECK early summer

Laophonte elongata BOECK

Laophonte minuta BOECK

Asellopsis intermedia T. SCOTT

Enhydrosoma propinquum (BRADY)

Tachidius discipes GIESBR.

Metis ignea PHILIPPI

Cirripedia:

Balanus crenatus BRUGUIÈRE

Up till now 2 species of acorn barnacles have been abundant in the Oosterschelde, viz. *Balanus crenatus* BRUG. and *Balanus balanoides* (L.). The latter lives in the intertidal zone, and the former below it. As most of our oysters live below the low water line, it is only *Balanus crenatus* which attaches itself in fair or large numbers to the oyster's shell. This has already been stated by HOEK (1884).

Balanus crenatus may give cause for anxiety when it settles down in great numbers. A profuse settling of barnacles on tile-collectors leaves little place for oyster spat, and forces many of the spat to grow around and over the barnacles, which results in irregularly shaped shells. Tiles covered with barnacles are usually subject to a more serious fouling

than those with a smooth surface. Profuse setting of barnacles on larger oysters forces the oystermen to clean the oysters before the latter are marketed, which involves a great deal of expensive manual labour and losses among the oysters through broken shells.

Barnacles did not occur in numbers worth mentioning on my experimental oysters at Yerseke.

Cumacea:

Bodotria scorpioides (MONTAGU)

Only one Cumacean species, *Bodotria scorpioides*, has been found on my experimental oysters:

Year	Oysters born in	Period
1941	1940	few only, September/October
1941	1939	few specimens in September and October
1942	1941	some in September
1942	1940	some in September
1943	1942	some from 13/9-19/10
1943	1941	September and October, one specimen 20/7

I did not find it in the years 1944 and 1945. I found it repeatedly in bottom samples taken in the tidal basin in which my trays with oysters were placed, especially in September and October. *Bodotria scorpioides* flourishes apparently in September and October.

Amphipoda:

Corophium acherusicum COSTA

Miss SCHIJFMA, who kindly identified the Amphipods collected by me, informed me that the specimens recorded from the Oosterschelde as *Corophium crassicorne* by HOEK (1884), belong in fact to the species *C. acherusicum* COSTA. It has also been found in the Waddenzee and in the former Zuiderzee.

I often found this gray-coloured Amphipod on oysters, where it lives in mud tubes between the scales of the flat valve. Their occurrence on my experimental oysters can be summarized as follows: (See page 116). On several samples of oysters from the plots or from trays in stations other than Yerseke, *Corophium acherusicum* did occur. As a rule there were about 5 specimens per 25 oysters. A greater number, 28 per 25 oysters was found on oysters from the Bergen op Zoom basin on 5-8-1942. Far greater numbers have been encountered between the scales of the flat valve of fairly large oysters kept in the station "Kijk-uit" Yerseke in the year 1940, viz. 6-9-1940, 27-9-1940, 7-11-1940. Sometimes about 10

Year	Oysters born in	Period
1941	1940	few in August, some in October
1941	1939	4/7 (1 juv.), 17/7 (5), later in the season from 3 to 6 per 50 oysters
1942	1941	increase in August, later from 2 to 5 per 50 oysters
1942	1940	few in July, increase late in August and in September; maximum 1 specimen per oyster
1943	1942	some in July, few in August, increase till 6 to 7 per 50 oysters in September
1943	1941	few in June and July, more in September and October. About 2 per 50 oysters
1944	1943	few only
1945	1944	few only

specimens were found on a single oyster. It is not clear why it occurred in far lower numbers in later years.

Egg-bearing individuals of *Corophium acherusicum* were collected on oysters at Yerseke, e.g. September, October, and November 1940, and in August, September, and October 1941.

Corophium acherusicum is said to feed on detritus only.

Microdeutopsis gryllotalpa COSTA

This species, somewhat larger than *Corophium acherusicum*, and not gray, but of an attractive green colour with pink legs, can be found in mud tubes between the scales of the oyster's flat valve, a habitat apparently appealing to a great many species of invertebrates. HOEK (1884) recorded the first Dutch specimens from this very habitat: "J'en recueillis plusieurs exemplaires dans la vase qui se trouve souvent dans les plis des coquilles d'huîtres."

On my experimental oysters at Yerseke it occurred as follows:

Year	Oysters born in	Period
1941	1940	few only
1941	1939	1 or 2 per 50 oysters throughout the season
1942	1941	a few in September
1942	1940	throughout the year 1 to 2 per 50 oysters
1943	1942	few only, more in September
1943	1941	Several in September and October. These oysters were brought from Bergen op Zoom to Yerseke on August 23rd and bore 15 to 20 specimens per 50 oysters on arrival
1944	1943	very few only
1945	1944	none

During my preliminary investigations I found it repeatedly on large oysters in the station "Kijk-uit", Yerseke: 6-9-1940, 17-9-1940, 6-10-1940, 7-11-1940.

Microdeutopsis appeared to occur in great numbers on oysters placed in the basin at Bergen op Zoom, as has already been indicated by the 1943 samples of oysters born in 1941, mentioned above. At Bergen op Zoom I recorded:

20-8-1941	21 per 25 oysters
22-7-1942	19 per 25 oysters
5-8-1942	50 per 25 oysters

Specimens bearing eggs have been recorded from samples taken at Yerseke in August, September, and October 1941.

Melita palmata (MONT.)

This species has often been found on oysters from the Bergen op Zoom basin, e.g. in September and October 1940, and on 20-8-1941 (9 specimens on 25 oysters). It does not live in a mud tube, but moves freely about on the shells. Only once did I find a juvenile specimen on my experimental oysters (9-6-1942).

Hyale nilssoni (RATHKE)

For the sake of completeness I mention having found an occasional specimen of *Hyale nilssoni* on an oyster, e.g. 10-9-1940 (1) station "Kijk-uit", Yerseke, 17-9-1940 (1) station "Kijk-uit", Yerseke, and none on my regular experimental series.

Cheirocratus sundevalli (RATHKE)

This species too has been collected a few times on oysters:

p. 224	13-10-1941 (2 specimens)
p. 302	13-10-1941 (1 specimen)

I never found it on my experimental oysters at Yerseke.

Gammarus locusta (L.)

As this species abounds in the Oosterschelde, especially among seaweeds, it need not surprise us that an occasional individual lost its way and landed on our oysters. The trays at Yerseke are only a few yards away from the *Fucus* vegetation:

Year	Oysters born in	Period
1941	1940	21/10 (1 specimen)
1942	1941	20/7 (1 specimen)
1942	1940	20/7 (7 specimens)
1943	1941	20/7 (1 specimen) and regularly since 30/8

I also found it on oysters from the Bergen op Zoom basin: 23-8-1943, 4 per 50 oysters.

Now it was these oysters from Bergen op Zoom which were brought to Yerseke on 23-8-1943 and used for the series 1943 born in 1941, mentioned above. It is noteworthy that *Gammarus* showed fairly high figures in several samples taken after the transplantation. This indicates that it is not necessarily an ephemeral visitor, but can stay in this habitat for a longer time.

Caprella linearis (L.)

Some individuals of *Caprella* have been found on my experimental oysters, viz.:

Year	Oysters born in	Period
1942	1940	30/6 (1), 8/7 (1)
1943	1942	27/7 (1)
1944	1943	19/7

The last mentioned specimen was found on a colony of *Bugula plumosa*. Can it be that *Caprella* feeds on *Bugula* too?

Decapoda:

Porcellana longicornis L.

HOEK (1884) has already recorded that this little crab is not rare in the Oosterschelde. I often found it in the tidal basin in the station "Kijk-uit", Yerseke. It shows marked fluctuations in its abundance. Some years we meet it only occasionally, while in other years it may be extremely abundant. The year 1943 was a very good year for *Porcellana*. In the month of July especially I counted great numbers in bottom samples taken in my tidal basin. Only in this year did I find it among my experimental oysters in the trays placed in this station. *Porcellana longicornis* is not typical for the oyster's epifauna, but this lively little crab spread all over the tidal basin in that particular summer.

Year	Oysters born in	Period
1941	1939	21/10 (2)
1942	1941	5/10 (1)
1943	1942	from 29/6 regularly a few specimens per sample
1943	1941	from 29/6 regularly some specimens per sample; up to 6 or 9 per 25 oysters

It is noteworthy, however, that BYTINSKI-SALZ (1935) found it in fair numbers on the shells of suspended oysters near Rovigno d'Istria.

Carcinides maenas (L.)

The shore crab is abundant and often a nuisance to the Dutch oystermen, because it likes to crack young oysters to devour the "fish". Spat, flattened out against a collector, cannot easily be killed by crabs, and few oysters older than about 16 months fall victim to the shore crab. Young oysters protruding from the collectors, and those recently detached and putting on growth, are especially vulnerable. This was already known to HOEK (1884). Damage by shore crabs is avoided very effectively by keeping the recently detached spat on trays for several months, a method practiced on a large scale by the Dutch oystermen.

Large shore crabs could not possibly get into my trays at Yerseke. Very young crabs did occur since they could get in freely through the meshes. I do not consider this species as typical of the oyster's epifauna. It abounded in the tidal basin at Yerseke, so that its occurrence in small numbers among the oysters in the trays could hardly be avoided:

Year	Oysters born in	Period
1941	1940	22/9 (6 juv.)
1941	1939	24/7 (4 juv.) since then a few regularly
1942	1941	since 8/7 a few regularly
1942	1940	14/7 (12 juv.), a few later
1943	1942	since 21/6 a few juvenile specimens regularly
1943	1941	since 21/6 a few regularly
1944	1943	since 28/6 a few regularly
1945	1944	few only since 25/6

It is noteworthy that small individuals of the shore crab always make their first appearance late in June or early in July.

ARACHNOIDEA

ACARI

Copidognathus fabricius LOHMANN

Occasionally I found in bottom samples and also in plankton samples taken close to the bottom of the Oosterschelde specimens of the Halacarid species *Copidognathus fabricius*. Through the help of the late Dr A. C. OUDEMANS specimens collected by me have been identified by the Halacarid specialist Dr K. VIETS (Bremen).

Sometimes I met them on my experimental oysters, where they crawled about clumsily like doddering old men:

Year	Oysters	Period
1942	1940	9/6 (1), 16/6 (1), 22/6 (1)
1943	1942	23/8 (1)

I never found one of the Halacarid species mentioned by ANDRÉ & LAMY (1930) as living on marine molluscs, oysters included, which are rightly or wrongly accused of parasitism.

PYCNOGONIDA

Pallene brevirostris JOHNSTON

Occasionally I found on my experimental oysters *Pallene brevirostris*, identified by the late Miss BUITENDIJK:

Year	Oysters born in	Period
1941	1940	10/9 (1), 6/10 (1)
1941	1939	10/7 (1)
1942	1940	8/9 (1), 15/9 (1)
1943	1942	5/7 (1), 27/9 (1)
1943	1941	5/7 (3), 27/7 (1)

There were none on my other series.

Anoplodactylus petiolatus (HODGE)

Of this species too, an occasional individual was collected on my experimental oysters at Yerseke:

Year	Oysters born in	Period
1941	1940	6/10 (1), 21/10 (1)
1941	1939	17/7 (1)
1942	1940	August and September a few
1943	1942	16/8–19/9 regularly a few

There were none on my other series.

Nymphon brevirostris HODGE

For the sake of completeness I record the finding of a single specimen of *Nymphon brevirostris* on my experimental oysters at Yerseke: Year 1941, oysters born in 1939, 4/7, 1 specimen.

PHYLUM MOLLUSCA

LORICATA

Lepidochiton cinereus L.

This small Chiton occurs in fair numbers in the Oosterschelde, crawling about on stones and shells, especially on the oyster beds on the intertidal flats East of Yerseke. We regularly find some of these little coat-of-mail shells attached to oysters or collectors. I never found them on my experimental oysters in the station "Kijk-uit", Yerseke.

GASTROPODA

Hydrobia ulvae (PENNANT)

For the sake of completeness I record that I twice found a specimen of *Hydrobia ulvae* on my experimental oysters: 1943, oysters born in 1942 2/6 (1), 8/6 (1), and none in my other series.

Apparently *Hydrobia*, being very abundant in many stations in the Oosterschelde, including the station "Kijk-uit", Yerseke, is a purely accidental visitor in this habitat.

Crepidula fornicata (L.)

The slipper limpet, is a real oyster pest in the Oosterschelde, settling down on old and fresh collector material, and thus taking the place meant for the oyster-spat. Locally it even forms entire beds. It was, however, rare in the station "Kijk-uit", Yerseke, and, as can be seen in the tables, only a very occasional *Crepidula* (e.g. 1945) settled on my experimental oysters. Though the larva of *Crepidula* abounds in the Oosterschelde plankton, it does not settle down and survive in every place where oysters or shells offer it a suitable substratum. We know of several districts in the Oosterschelde, where *Crepidula* may settle in great numbers, but where it always disappears within a few weeks. Practical oystermen claim that those beds are too "sharp", i.e. many fine angular sand grains are swept around there in the water layers close to the bottom. It is assumed that young *Crepidula* cannot survive on such grounds. Scientific investigations have not yet been carried out on the causal relation between the "sharpness" of a ground and the survival rate of young *Crepidula*, tiny oysters, and other molluscs.

Tergipes despectus (JOHNSTON).

For the sake of completeness I mention that one specimen of this Nudi-branch Gastropod, identified by Dr H. ENGEL, has been found on my oysters at Yerseke: 1942, oysters born in 1940, 30/6 (1).

LAMELLIBRANCHIATA

Mytilus edulis L.

Though tremendous quantities of mussels are grown in Zealand waters, and though the larvae of *Mytilus* usually abound in the plankton of the Oosterschelde, spatfall of *Mytilus* occurs only locally and occasionally there. We know very little about the conditions which suit the mature mussel larvae and the early benthonic stages of *Mytilus edulis*. Judging from experience gained with the French "bouchots" and from the opinion of our practical oystermen, we are inclined to assume that the presence of Hydroids is of the greatest practical importance in the settling down of mussel larvae. Though occasional young mussels may settle down in many places (e.g. in the trays of the oystermen, placed off Yerseke, and sometimes on tile-collectors), mass-settlement of mussel-seed is exceptional in the Basin of the Oosterschelde. There are old records of mussel-seed covering oysters there in such quantities that the oysters were threatened with smothering. In recent years I heard of mussel-seed settling profusely on oysters in only one plot. Unfortunately I heard of it too late to investigate whether or not a dense growth of Hydroids had preceded the settling of *Mytilus*. Buoys floating in the immediate vicinity of the oyster-beds, the anchor-chains of those buoys, and similar objects, may be crammed with mussel-seed while the oysters nearby do not suffer at all. The officers of the Zealand Fishery Police claim that in those cases too, profuse settling of Hydroids on the iron substrata preceded the mass-attachment of mussel-seed. While investigating whether or not development of beds of seed-mussels is to be expected, the above mentioned officers look for Hydroids and feel with their fingers for the still very tiny mussels.

A few specimens of *Mytilus edulis* settled on my experimental oysters:

Year	Oysters born in	Period
1942	1941	from 30/6 regularly a few
1942	1940	8/7 (1), 28/7 (1)

Anomia ephippium L.

In the French oyster districts, especially in Brittany, *Anomia ephippium* is a real oyster pest, settling down on the collectors, and thus taking the place meant for the oyster spat. Others settle down on, and thus possibly compete for food with, the oyster. In detaching the oyster spat from the tiles most of those "luisettes" are left behind. Those which are detached with the young oysters die soon for lack of substratum.

Attached to French oysters, *Anomia ephippium*, known among the Dutch oystermen as the "French slipper", has been introduced into Dutch waters. It does not thrive there as a rule and its reproduction is exceptional. In December 1937 I found a young specimen attached to a Dutch tile collector. After the warm summer of 1947 young specimens of *Anomia ephippium* could be found in fair numbers on mussel shells broadcast on the plots as collectors (KORRINGA, 1948). I do not believe that the hydrographical conditions prevailing in the Ooster schelde suit *Anomia ephippium*.

Ostrea edulis L.

On natural oysterbeds the new growth shoots of the adult oysters are probably the only clean and hard objects oyster larvae do encounter. The new grown shell of an oyster therefore is the most natural collector for the young spat of *Ostrea edulis*. Young specimens of *Ostrea edulis* did occasionally settle down on my experimental oysters at Yerseke, I did not, however, keep a constant record of this, so that *Ostrea edulis* cannot be found in the tables. Their number was small. The warm summers of 1941 and 1944 gave a fair set.

Tapes pullastra (MONT.)

Young and very young specimens of *Tapes pullastra* can be found attached with byssus-threads to many different objects. It occurs on tile-collectors, and also on the lime coated glass slides we use to measure the intensity of the setting of oyster spat. Sometimes an occasional specimen, very small as a rule, attaches itself to the shell of an oyster.

On my experimental oysters I found it on 1-9-1941 on oysters born in 1940. I also found it on oysters kept in a tray at p. 551 (21-10-1940, 5 on 25 oysters), and on oysters taken from p. 417 (21-10-1940, 2 on 10 oysters). Its occurrence in the biocoenosis of oyster-shells is no doubt of limited ecological importance, and of short duration only, as *Tapes* burrows in the soil eventually.

PHYLUM TENTACULATA

BRYOZOA ECTOPROCTA

Bugula plumosa PALLAS

The vertical walls in the tidal basin used at Yerseke showed a profuse growth of *Bugula plumosa*. Sometimes I detected the colonies of this Bryozoan on my experimental oysters, viz.:

Year	Oysters born in	Period
1942	1941	few but regularly since 8/7
1942	1940	22/9, 29/9
1943	1942	few but regularly
1943	1941	8/6, 23/8, 27/9, 6/10
1944	1943	few but regularly since 22/6
1945	1944	very few only

These data and the occurrence on vertical walls suggest that *Bugula* larvae prefer to settle on relatively clean objects. Young oysters offer a higher percentage of clean new shell growth than older oysters do. Settlement of *Bugula*, and subsequent development of its colonies occurred during the summer season. I rarely or never found *Bugula* on oysters taken in other stations in the Oosterschelde.

BRYOZOA ENDOPROCTA

Barentsia gracilis SARS

Occasionally I found colonies of an Endoproct Bryozoan on my oysters, which have been identified as *Barentsia gracilis* by Dr A. G. VORSTMAN. Observation under water reveals that the individuals of a *Barentsia* colony often jerk their heads, especially when disturbed.

On my experimental oysters I found *Barentsia* on the following occasions:

Year	Oysters born in	Period
1941	1940	24/7-10/9
1942	1941	22/6-1/9 regularly a few
1942	1940	regularly a few
1943	1942	15/6-29/6
1945	1944	18/6-25/6

and none on my other series.

New colonies evidently are formed in early summer. Rarely or never did I find *Barentsia* on oysters taken in other stations, but it does occur on tile-collectors occasionally.

PHYLUM ECHINODERMATA

ASTEROIDEA

Asterias rubens L.

The common starfish is very abundant in the Zealand waters as elsewhere along the Dutch coast. Only through regular cleaning of the beds do the mussel farmers manage to limit the damage caused by *Asterias rubens*. Though the starfish does occur on the Dutch oyster beds, the number of adult oysters devoured is no cause for serious anxiety. The starfish apparently prefers mussels for its diet, or encounters less difficulty in opening them. Serious damage can be done by young and very young starfishes among the tiny oyster spat on the tile-collectors. A regular inspection of the collectors is a necessity, and in case of abundance handpicking of starfishes pays.

Important points in the biology of the starfish are still rather obscure. I presume that a starfish paralyses its victim at the very moment when the mollusc – embraced by the starfish – opens its shells a little bit to find out whether the danger is still there. Force exercised by the ambulacral feet presumably is of minor importance only. Our fishermen claim that starfishes migrate to other feeding grounds by producing gas and floating along the surface. Floating starfishes, containing a gas-bubble have often been observed, sometimes in great numbers together. It is not yet clear whether this is a normal and reversible state or a pathological condition, leading to the starfish's death.

Very occasionally I found some young starfishes on my experimental oysters:

Year	Oysters born in	Period
1945	1944	18/6 (3), 3/7 (1), 24/7 (3), 13/8 (1)

There were none on my other series.

That young starfishes were especially abundant in the year 1945 can be explained by the occurrence of unusually large numbers of adult starfishes in the Zealand waters which no doubt produced countless starfish larvae in the warm summer of 1945. Lack of fuel and of adequately equipped vessels cut down starfish control in the war years. The Zealand mussel farmers had been totally unable to clean their beds from starfishes in the season 1944-1945, because of war conditions, which turned the Zealand waters into a "no-man's-land" for many months. Some time after the termination of hostilities the mussel beds were cleaned of starfishes by a well co-ordinated simultaneous dred-

ging, in which all available vessels participated. That broke the temporary domination of starfishes on the mussel beds. Since then the mussel farmers have been able to keep their numbers well below the danger level. I therefore disagree with BURKENROAD (1946), who suggests that fluctuations in abundance of starfish are predominantly a natural phenomenon, and that measures of control have but a very limited effect.

Ophiothrix fragilis (ABILDGAARD)

An occasional young individual of the brittle-star has been found on my experimental oysters. No doubt it is an accidental visitor in this habitat.

Year	Oysters	Period
1941	1940	21/10 (1 juv.)
1941	1939	21/10 (2 juv.)
1943	1941	10/9 (1 juv.)

PHYLUM CHORDATA

TUNICATA

Attached to oysters and collectors in the Oosterschelde one may find the following Tunicates:

Ascidella aspersa (O. F. MÜLLER)

Molgula tubifera (ØRSTED)

Ciona intestinalis L.

Botryllus Schlosseri (PALLAS)

Ascidella aspersa is often very numerous and then may smother the young oyster spat on tiles and shell-collectors. It is therefore considered as an oyster pest. The abundance of *Ascidella* varies considerably, however, and in many years it is hardly noticed by the oystermen. I never found it attached to my experimental oysters at Yerseke.

Molgula tubifera is rarer than *Ascidella aspersa*, and occurs occasionally in single individuals on tile-collectors. I did not find it on my experimental oysters.

Ciona intestinalis. On October 16, 1950, I detected a fair number of *Ciona intestinalis*, attached to lime-coated tile collectors, placed in the Zandkreek. I had never seen it before from Dutch waters. I did not find it on my experimental oysters.

Botryllus Schlosseri may grow in large colonies on tile collectors and on the wood and wire netting of oyster trays. Sometimes it settles also on

oyster shells. *Botryllus* may smother young oysters, and therefore is listed among the oyster pests by the Dutch oystermen. It is my impression that it settles by preference on oysters and trays in stations where low current velocities prevail for many hours.

I found it on my experimental oysters fairly regularly in the year 1943, on oysters born in 1941. I did not find it on my oysters in other years, but often encountered it on tiles and trays in other stations. The oyster basin at Bergen op Zoom is notorious for the abundance of *Botryllus*.

DISCUSSION

The present investigations revealed that exterior surfaces of the shells of living oysters may be inhabited by a fauna both rich in species and individuals. Reconsidering the data collected in the tables, I believe it is no exaggeration to say that the epifauna of the oyster is amazingly rich. This is the more surprising since the investigations were carried out in the years 1940–1945 inclusive, in which period we had to endure several unusually severe winters, viz.: 1939–1940, 1940–1941, and 1941–1942. As can be seen in the temperature tables, water temperatures came down for prolonged periods to levels far below the average. Huge quantities of ice floes overturned the superficial layers of many shallow grounds and scraped the sea-weed from the dykes. These winters seriously affected a number of marine vertebrates and invertebrates otherwise common in Dutch inshore waters. The members of the oyster's epifauna discussed in this paper most probably were not affected noticeably by these severe winters, for the years 1944 and 1945 were by no means richer in species or individuals than the years immediately following those winters.

It is interesting to note that the oyster's epifauna is not just a small scale representation of the usual bottom fauna of the district concerned. That species adapted to a life in sand or mud deposits do not consider the oyster's shell as a suitable substratum, is not surprising. Still, occasional individuals of such species may be found on the oyster's shell, especially in the very modest deposits of mud and sand between the scales of the oyster's flat valve. I presume that young individuals of such species do recognize whether or not the type of sediment found provides micro-ecological conditions suitable for the species, but that they fail to recognize whether there is enough of it for the establishment of a normal existence.

More interesting is the fact that several species abound on oyster shells, but have rarely or never been collected outside this very special habitat. Some species, thus far never found in Dutch waters, or con-

sidered as rare, appear to live in great or moderate numbers as epibionts of the oyster. It is difficult to see why. Evidence has been put forward that the factor of shelter is predominant in this respect.

As my investigations were carried on during several years, and as many samples of oysters from other stations have been included, I believe that the picture given of the oyster's epifauna in the Oosterschelde is fairly complete so far as the listing of species and the enumeration of individuals goes. I do not believe that the extension of the investigations over still more years or the inclusion of more stations in the Zealand waters could have brought about material changes in the picture given. It is to be expected that an epifauna of a different composition will occur in other oyster regions. The oysters of the French districts, for example, will most probably be inhabited by several species which cannot endure the low water-temperatures recorded in winter at Yerseke. Other ecological factors too will cause differences in the oyster's epifauna. In many of the French districts the oysters are grown on intertidal flats, which is very unsuitable for many of the species of epibionts. Oysters from the scanty remains of the French natural oyster beds usually live in deeper water, but are often subject to far greater changes in salinity than the Oosterschelde oysters, which may reduce the number of species of epibionts. Very special conditions prevail among the oysters hanging from racks in the Etang de Thau on the French Mediterranean coast. Ascidians predominate there. Also oysters grown in suspended trays in Norwegian waters will show an epifauna different from that of the oysters in the Oosterschelde. An occasional observation has shown me that Ascidians, Hydroids and Nudibranch Gastropods abound there on the oysters.

Though I claim that the picture given will be fairly complete for the district under consideration so far as the number of species and individuals go, I must confess my ignorance on many points of the economics of the system studied. I do not yet understand how such an amazingly rich epifauna can support itself on the shells of the oyster. I was unable to find an answer to many of the questions raised:

CO₂-assimilation by green plants residing on the shells of the oysters is probably not of any appreciable importance in the economics of the biocoenosis studied. Plants bearing chlorophyll or similar pigments have rarely or never been encountered on the experimental oysters. The oysters lived in dim light only, as the lids of the trays became clogged up and smothered by all kinds of growths and deposits. The oysters taken from the plots came from fairly deep levels where light is subdued owing to the rather turbid water of the Oosterschelde.

The possibility that the oyster itself contributes to the fertility of the system under consideration by putting down on the shell its pseudo-

faeces and faeces, is limited, for those products are not usually deposited on the shell and only in overcrowded trays placed in rather quiet waters have they a chance to drop and stay on the shells of other oysters.

It is probable that few of the members of the oyster's epifauna use the oyster's shell as a shelter and base of operations only, and crawl away from the oyster in search of food. A comparison of oysters kept in trays with those from the plots of the oystermen indicates that this can hardly be a factor of any importance.

Though several of the more abundant inhabitants have been studied in greater detail, not the slightest indication has been obtained that any of those species finds its source of food in the living tissues of the oyster itself; so far as I am aware parasitism is not in question.

The epibionts of the oyster, which secure their food in some way or other from the plankton of the surrounding water are limited in numbers. Of the more important plankton feeders I can mention *Folliculina*, *Haliclone limbata*, *scyphistoma* of *Aurelia aurita*, *Polydora ciliata*, and *Barentsia gracilis*. It is highly improbable that this group provides the broad food basis necessary for all the other members of the oyster's epifauna, since in other stations with an equally rich epifauna *Haliclone*, *Aurelia-scyphistoma* and *Barentsia* did not occur. It seems hardly possible that *Folliculina* and *Polydora* can feed such a vast number of predators as are found on the shells of the oyster.

It is difficult to say in the present state of our knowledge which of the other creatures are purely predatory, and which feed on detritus. Some detritus is deposited on the shells of oysters by the tidal currents. Even where strong tidal currents prevail during several hours a day, some silt loaded with detritus particles will be deposited on the shell of the oyster. It is possible that this is a source of food of some importance in the system under consideration.

Though several members of the epifauna are definitely of the predatory type, I do not know on which victim they specialize. No evidence has been collected to show that the predominance of certain species brought about a noticeable decline in the numbers of other species. Even huge numbers of *Aurelia* polyps, armed with their dangerous nematocysts, did not seem to have a deleterious effect on other members of the oyster's epifauna. Though the many different species live very close together on the oyster's shell, mutual relations were not very obvious. Though some species did exceptionally well in certain years, it is difficult to ascribe this to favorable temperature conditions, abundance of food, or lack of predators.

Only of two members of the oyster's epifauna can it be said that they may give cause for anxiety from the point of view the oyster, e.g. *Clione celata* and *Polydora ciliata*. Both may dig their burrows so deep or be so

numerous in the shells that the oyster's well-being is endangered. *Polydora hoplura*, which crawls in between the mantle and the shell of the oyster, so far does not occur regularly in the Oosterschelde.

Summarizing I must confess that I have but a poor understanding of the economic system on which the surprisingly rich epifauna of the oyster's shell is based. The factor "shelter" no doubt is of primary importance in the system, but besides that there must be sufficient food available to feed the many creatures living there. I can hardly believe that the number of filter feeders and detritus consumers encountered is sufficient to feed the many predators found.

We should add, however, that it has always proved to be extremely difficult to obtain a good quantitative picture of the food balance in an inshore marine biocoenosis. Our knowledge of the food habits of marine invertebrates is still very fragmentary. We know little or nothing about the daily requirements of the different species. What do we know about the achievements of filter feeders? Do we possess any quantitative data on the amount of detritus available in inshore waters, and on the digestibility of the different components of this detritus? It is certainly doubtful whether the fragments of old peat, so often encountered in the Oosterschelde plankton, are of any use to invertebrates. We are inclined to overestimate the importance of the net-plankton and to underestimate that of the nanno-plankton. We ignore the presence and importance of minute particles of organic material, not detected with the microscope, but possibly highly interesting to several marine invertebrates. As we are moreover too easily inclined to think in terrestrial proportions, we can hardly hope to obtain a complete quantitative picture of the food balance of an inshore marine biocoenosis in the present state of our knowledge.

The present study does contribute materially to our knowledge of the season and methods of reproduction of several of the members of the oyster's epifauna.

SUMMARY

Field investigations carried out in the Oosterschelde (Holland) on the epidemiology of shell disease in *Ostrea edulis*, revealed the presence of a rich fauna on the shells of living oysters. Invertebrate animals from many different groups appeared to belong to the oyster's epifauna. Polychaete worms predominated both in numbers of species and individuals.

Quantitative data from weekly samples were collected during 5 consecutive summer seasons. These data provide interesting information on the season and methods of reproduction of the species concerned.

The oyster's epifauna differs noticeably from the usual bottom fauna in the district under consideration. Several species appeared to live by preference in this very special habitat.

Evidence is adduced that the majority of the members of the oyster's epifauna come from the plankton. Experiments with wooden boxes fitted with wire gauze of different mesh size, demonstrated that many of the planktonic larvae do not hesitate to crawl through narrow apertures, and that few, if any, animals settle down on oysters as full grown adult individuals. The members of the oyster's epifauna are not accidental visitors, but permanent residents.

Experiments with living oysters and shells of dead oysters demonstrated that adequate shelter is the most important factor in the habitat under consideration. No evidence could be adduced that any of the members of the oyster's epifauna lives parasitically on the living tissues of the oyster. There is no proof that the oyster contributes materially to the fertility of the system by depositing faeces and pseudo-faeces.

An annotated list of species encountered is given. Species of microscopical dimensions are not included. So far as the quantitative data collected in the tables allow, and so far as other observations and information go, conclusions have been drawn on the season of reproduction and on other biological topics of the species concerned. In some cases morphological details have been given.

A complete picture of the food balance of the system studied cannot yet be given.

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	3 (juv.)	2 (juv.)	10	44	54	45	41	15	11	17	25	21	17	55	27	5
<i>Pholoe minuta</i>	—	—	17	36	40	73	70	41	81	110	86	90	70	95	100	46
<i>Phyllodoce maculata</i>	—	—	—	—	3	3	—	—	1	1	—	1	1	—	—	—
<i>Eulalia viridis</i>	—	1 (juv.)	—	2	5	—	1	—	2	1	—	1	1	3	3	—
<i>Eulalia sanguinea</i>	—	—	6	10	8	2	9	2	2	3	5	3	2	—	—	1
<i>Eteone longa</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	—
<i>Eteone picta</i>	—	2	2	—	1	—	—	—	—	1	—	2	1	—	—	—
<i>Autolytus cornutus</i>	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Autolytus aurantiacus</i>	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Nereis succinea</i>	1	4	29	15	19	4	17	2	2	7	2	6	1	5	4	—
<i>Platynereis Dumerilii</i>	—	—	5 (juv.)	10	13	6	10	9	18	11	13	15	5	10	2	1
<i>Polydora ciliata</i>	—	—	—	—	—	—	—	—	—	—	—	—	6	2	2	—
<i>Polydora ciliata</i>	2	24	20	26	27	15	15	12	14	14	15	10	5	5	3	—
<i>Arenicola marina</i>	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Amphitrite Johnstoni</i>	1 (juv.)	—	—	1 (juv.)	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda:																
<i>Loxoconcha impressa</i>	—	—	—	—	—	—	—	—	—	—	1	2	6	24	2	—
Harpactida:																
<i>Longipedia minor</i>	—	+	+	+	+	+	+	+	++	++	++	++	++	++	+	+
Cumacra:																
<i>Bodotria scirpioides</i>	—	—	—	—	—	—	—	—	—	1	—	—	—	2	—	—
Amphipoda:																
<i>Corophium acherusicum</i>	—	—	1	—	—	1	3	1	1	—	—	—	2	9	1	—
<i>Microdeutopsis gryllotalpa</i>	—	—	—	—	—	1	—	—	—	1	1	—	—	1	1	1
<i>Gammarus locusta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Decapoda:																
<i>Carcinides maenas</i>	—	—	—	—	—	—	—	—	—	—	6 (juv.)	—	—	—	—	—
Pycnogonida:																
<i>Pallene brevirostris</i>	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—
<i>Anoplodactylus petiolatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Bryozoa:																
<i>Barentsia gracilis</i>	—	—	—	—	+	+	+	+	+	+	+	—	—	—	—	—
Echinodermata:																
<i>Ophiothrix fragilis</i>	—	—	—	—	+	+	+	+	+	+	—	—	—	—	—	—
														1 (juv.)		

TABLE V

Yerseke, "Kijk-uit", 1941. Epifauna of samples of 50 oysters, born in 1939, and kept on trays.
 Oysters kept on trays at Yerseke in 1940 Winter 1940-1941 in basin at Bergen op Zoom. Replaced at Yerseke 30 5-1941
 Transferred to Bergen op Zoom 21-10-1941

— absent, + present but rare, ++ moderate numbers, +++ abundant

Date	20/5	16/6	25/6	4/7	10/7	17/7	24/7	31/7	11/8	18/8	25/8	1/9	10/9	22/9	6/10	21/10	4/11	4/12
Water temperature °C	12.0	16.0	21.3	19.9	22.7	20.7	20.2	18.9	17.5	17.0	16.8	16.8	16.8	15.7	15.0	11.7	5.7	4.0
Specific weight 17½ °C	1.0195	1.0205	1.0215	1.0215	1.0215	1.021	1.0205	1.0205	1.0205	1.0205	1.0200	1.0200	1.0200	1.0210	1.0210	1.0210	1.0205	1.0195
Are of shell surface per oyster (cm²)	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	62	—	—
Foraminifera:																		
<i>Gilithionina heinckei</i>					+	++	++	+	+	+	+	++	++	++	++	++	++	+
Ciliata:																		
<i>Folliculina ampulla</i>	—	—	+	+	+	++	+	+	+	+	++	++	++	++	++	++	++	+
Porifera:																		
<i>Halidone limbata</i>	—	—	—	—	—	+	+	+	+	++ (g)	++ (g)	(g)	(g)	++ (g)	(g)	(g)	++ (g)	+
Coelenterata:																		
<i>Aurelia aurita</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Diadumene cincta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Turbellaria:																		
<i>Plagiosiomum vittatum</i>	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Nemertini:																		
<i>Lineus ruber</i>	1	2	1	3	9	3	6	3	1	2	9	—	3	2	2	3	2	2
<i>Tetrastemma flavidum</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nematoda:																		
<i>Anticoma limatis</i>	—	1 ♀	—	1 ♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thoracostoma trichodes</i>	—	1 ♀	—	2 (juv.)	—	4 (juv.)	4 (juv.)	2 (juv.)	1 (juv.)	—	3 (juv.)	—	2 (juv.)	1 (juv.)	—	—	—	—
<i>Enoplus communis</i>	1 ♀	1 (juv.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Enoplus brevis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oncholaimus skauensis</i>	1 ♂ 1 ♀ 1 ♂ 3 ♀	—	—	—	1 ♀	—	1 ♀	1 ♀	—	—	—	—	—	—	—	—	—	—
<i>Metoncholaimus pristiurus</i>	2 ♂ 1 ♀ 1 (juv.)	1 (juv.)	—	—	1 ♀	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eurytemora filiforme</i>	—	—	1 ♂	—	—	—	1 (juv.)	—	—	—	—	—	—	—	—	—	—	—
<i>Symphlocostoma longicollis</i>	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Enchelidium marinum</i>	1 ♂ 1 ♀	—	—	—	1 ♂	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Euchromadora vulgaris</i>	3 ♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2 ♂
Polychaeta:																		
<i>Lebidonotus squamatus</i>	—	—	1 (juv.)	5	7 (juv.)	17	7	7	8	9	12	7	8	4	15	19	16	10

<i>Hamulolae imbricata</i>	—	—	2 (juv.)	17 (juv.)	36 (juv.)	—	3	71	71	82	71	—	1	58	78	—	54	—	1	43	84	1	—	18	9
<i>Hammolae imbr.</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pholoe minuta</i>	78	45	—	37	30	112 (27 ad.)	160 (20 ad.)	184 (14 ad.)	204 (9 ad.)	145 (5 ad.)	175 (2 ad.)	173 (1 ad.)	265	190	—	1	5	5	—	—	2	—	130	105	63
<i>Phyllodoce maculata</i>	—	1 (juv.)	5	5	5	4	2	2	2	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eulalia viridis</i>	3	2	3	4	4	2	2	2	3	5	7	1	5	5	8	1	5	3	1	—	—	—	—	—	—
<i>Eulalia sanguinea</i>	3	3	1	1	20 (juv.)	5 (juv.)	9 (juv.)	10 (2 ad.)	10 (1 ad.)	2	7 (juv.)	5	8	4	2	4	1	1	3	—	—	—	—	—	—
<i>Eteone longa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eteone picta</i>	—	2	4	4	1	1	1	1	2	1	1	1	1	—	—	—	1	2	—	—	—	—	—	—	—
<i>Autolytus cornutus</i>	—	—	1	1	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Autolytus aumticius</i>	—	—	14	49	—	29	28	29	7	19	14	11	16	5	5	22	8	7	6	—	—	—	—	—	—
<i>Nereis succinea</i>	—	—	1	2	—	—	7 (juv.)	8 (juv.)	7 (juv.)	13 (7 juv.)	13	14	14	12	11	18	6	4	5	—	—	—	—	—	—
<i>Platyeris Dumerilii</i>	—	—	—	—	—	1	—	—	—	—	1	1	—	—	2	1	1	1	—	—	—	—	—	—	—
<i>Scoloplos armiger</i>	1 (juv.)	—	—	—	—	40	51	32	12	8	13	6	14	3	9	2	7	3	—	—	—	—	—	—	—
<i>Polydora ciliata</i>	53	43	48	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tharyx multibranchiis</i>	—	—	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Capitella capitata</i>	1	—	1	5	—	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arenicola marina</i>	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pectinaria koreni</i>	—	—	1 (juv.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oligochaeta:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Paranis littoralis</i>	70	18	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ostracoda:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Loxoconcha impressa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	5	90	7	8	—	—	—	—	—	—
<i>Harpacticida:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Longipedia minor</i>	+	++	++	++	++	+	+	+	+	+	+	+	++	++	++	++	++	++	++	++	++	++	++	++	++
<i>Cumacea:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bodotria scorpoides</i>	—	—	—	—	—	—	—	—	—	—	—	—	1	1	5	3	5	—	—	—	—	—	—	—	—
<i>Amphipoda:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Corophium acherusicum</i>	—	—	—	—	1 (juv.)	—	5	2	3	3	3	—	4	3	2	3	6	6	—	—	—	—	—	—	—
<i>Microdeutopsis gryllotalpa</i>	—	—	1 ♀	—	—	1 ♂	2	2	—	1	—	—	—	2	2	4	—	1	1	—	—	—	—	—	—
<i>Decapoda:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Porcellana longiconis</i>	—	—	—	—	—	—	—	4 (juv.)	—	—	3 (juv.)	2 (juv.)	—	2 (juv.)	—	2 (juv.)	—	—	—	—	2	—	—	—	—
<i>Carcinides maenas</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pycnogonida:</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pallene brevisstris</i>	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anoplodactylus petiolatus</i>	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Nymphon brevisstris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Echinodermata:</i>	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ophiothrix fragilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Yerseke, "Kijk-uit", 1942. Epifauna of samples of 50 oysters, born in 1941, and kept on trays. Oysters placed at Yerseke 4 6 1942. Trays with oysters transferred to the Bergen op Zoom oyster basin 12-10-1942

— absent, + present but rare, ++ moderate numbers, +++ abundant

[illegible]

Yerseke, "Kijk-wit", 1942. Epifauna of samples of 50 oysters, born in 1940, and kept on trays. Oysters kept on trays at Yerseke in 1941, from 30/5 to 21/10. Winter 1941-1942 in basin at Bergen op Zoom. Replaced at Yerseke 4-6-1942. Transferred to Bergen op Zoom 12-10-1942.

— absent, + present but rare, ++ moderate numbers, +++ abundant

Date	9/6	16/6	22/6	30/6	8/7	11/7	20/7	28/7	3/8	18/8	25/8	1/9	8/9	15/9	22/9	29/9
Water temperature °C	16.3°	15.7°	17.2°	18.5°	17.5°	17.7°	16.8°	17.3°	18.5°	19.1°	19.4°	20.7°	18.1°	18.7°	15.7°	14.4°
Specific weight 17½ °C	1.0205	1.0210	1.0215	1.0215	1.0215	1.0210	1.0205	1.0210	1.0215	1.0215	1.0215	1.0215	1.0215	1.0215	1.0205	1.0205
Area of shell surface per oyster (cm²)	42													54		
<hr/>																
Foraminifera:																
<i>Crithionina heuckei</i>	—	—	+		++											+
Ciliata:																
<i>Folliculina ampulla</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Porifera:																
<i>Sycon ciliatum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Halidone limbata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coelenterata:																
<i>Tubularia larynx</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Laomedea loveni</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aurelia aurita</i>	—	—	—	—	—	—	—	—	++	++	—	—	—	—	—	—
<i>Sagartia anguicoma</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Diadumene cincta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Turbellaria:																
<i>Plagiosiomum vittatum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nemertini:																
<i>Lineus ruber</i>	1	2	1	1	3	3	—	2	2	2	4	2	2	2	2	—
<i>Tetrasemma flavidum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nematoda:																
<i>Enoplus communis</i>	—	—	1 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	—	—	—	—	—	—	—	—	—
<i>Oncholaimus skarensis</i>	—	1 ♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Enchelidium marinum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cyatholaimus demani</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polychaeta:																
<i>Leptodolus squanatus</i>	1 (juv.)	—	—	4 (juv.)	13	19	13	10	8	14	20	26	46	30	26	54
					(10 juv.)											
<i>Harmoloe imbricata</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Harmoloe impar</i>	3 (juv.)	5 (juv.)	1	26	30	52	91	90	66	82	114	162	242	190	192	292
<i>Pholoe minuta</i>	10	7	12	18	57	63	65	101	190	176	310	180	163	150	206	196

<i>Phytolacca maculata</i>	1 (juv.)	1	2	2	10	3	5	6	6	6	2	2	2	4	2	—
<i>Eutalia viridis</i>	—	—	—	—	2	1	—	—	2	—	—	—	10	2	—	4
<i>Eutalia sanguinea</i>	—	2	2	5	45 (39 juv.)	39	46	14	8	—	34	—	40	22	48	58
<i>Eteone longa</i>	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Autolytus cornutus</i>	—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	—
<i>Autolytus aurantiacus</i>	—	—	10	19	24	23	60	46	32	—	58	26	26	16	40	40
<i>Nereis succinea</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
<i>Platyeris Dumerilii</i>	—	—	—	—	1	—	—	—	12	—	40	8	8	4	6	8
<i>Polydora ciliata</i>	14	34	58	57	75	43	40	44	—	—	—	—	—	—	—	—
<i>Capitella capitata</i>	—	—	1 (juv.)	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arenicola marina</i>	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Amphitrite Johnstoni</i>	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oligochaeta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Paranais littoralis</i>	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	10
<i>Loxoconcha impressa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haracticida:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Longipedia minor</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cumacea:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bodotria scorpioides</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Corophium acherusicum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Microdeutopsis gryllotalpa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Melita palmata</i>	1 (juv.)	—	—	—	1	1	—	2	2	—	—	—	—	—	36	44
<i>Gammarus locusta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	4
<i>Caprella linearis</i>	—	—	—	—	1 (juv.)	—	7	—	—	—	—	—	—	—	—	—
Decapoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carcinides maenas</i>	—	—	—	—	—	12 (juv.)	8 (juv.)	6 (juv.)	6 (juv.)	6 (juv.)	—	—	6 (juv.)	8 (juv.)	6 (juv.)	2 (juv.)
Acari:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Copidognathus fabricius</i>	1	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Pycnogonida:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pallene brevivestris</i>	—	—	—	—	—	—	—	—	1	—	—	1	1	1	—	—
<i>Anphlodactylus petiolatus</i>	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Mollusca:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tegipes despectus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Mytilus edulis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bryozoa:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bugula plumosa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Barentsia gracilis</i>	+	+	+	+	+	+	+	+	+	+	+	—	—	+	+	+

Yerseke, "Kijk-vut", 1943. Epifauna of samples of 50 oysters, born in 1942, and kept on trays.
Oysters placed at Yerseke 28-5-1943. Trays with oysters transferred to the Bergen op Zoom oyster basin 14 10 1943
— absent, + present but rare, ++ moderate numbers, +++ abundant

Date	2/6	8, 6	15/6	21/6	29/6	5/7	14/7	20/7	27/7	2, 8	16, 8	23/8	30, 8	6, 9	13, 9	20, 9	27, 9	6, 10	19/10
Water temperature °C	16.2 ⁵	15.1 ⁰	16.8 ²	17.2 ²	17.6 ⁰	18.2 ⁰	17.4 ⁰	19.2 ⁰	19.4 ⁰	21.5 ⁵	17.9 ³	19.7	17.6 ¹	18.0 ⁰	18.0	16.0	13.7	13.7 ⁵	12.9 ⁰
Specific weight 17½ °C	1.0215	1.0215	1.0222	1.0215	1.0215	1.0225	1.0225	1.0235	1.0235	1.0215	1.0210	1.0230	1.0225	1.0230	1.0230	1.0225	1.0235	1.0235	1.0220
Area of shell surface per oyster (cm ²)	13	10	15	13	18	23	21	29	31	34	39	47	47	45	49	51	47	54	54
Foraminifera:																			
<i>Grithionina heinckei</i> . . .	—	—	—	+	++	+++	++	++	++	++	+	+	+	+	+	+	+	+	+
Ciliata:																			
<i>Folliculina ampulla</i> . . .	++	++	++	++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Porifera:																			
<i>Sycon ciliatum</i>	—	—	—	—	—	—	+	+	+	+	+	+	++	++	++	++	++	++	++
<i>Halicione limbata</i>	—	—	—	—	—	—	—	—	—	+	+	+	++	++	++	++	++	++	++
Coelenterata:																			
<i>Aurelia aurita</i>	—	—	—	—	+	+	+	++	++	++	++	++	++	++	++	++	++	++	++
<i>Sagartia anguicoma</i>	2	—	—	—	+	—	1	2	1	2	—	—	—	+	+	+	+	+	+
<i>Diadumene cincta</i>	—	—	+	+	+	+	—	—	—	—	+	+	+	—	+	+	—	+	+
Nemertini:																			
<i>Lineus ruber</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
<i>Tetrasemma flavidum</i> . . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Nematoda:																			
<i>Thoracostoma trichodes</i> . .	1 ♀	—	—	—	—	—	1 ♀	—	—	—	—	—	—	—	—	—	—	—	—
<i>Enoplus communis</i>	2 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	1 (juv.)	3 (juv.)	3 (juv.)	2 (juv.)	—	—	2 (juv.)	—	1 (juv.)	—	1 (juv.)	1 (juv.)	—
<i>Oncholaimus skauensis</i> . . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Melonchlamys pristinurus</i> . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eurytemora filiforme</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Præacanthionchus punctatus</i> .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Euchromodora vulgaris</i> . . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Monoposthia costata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polychaeta:																			
<i>Lepidonotus squamatus</i> . . .	—	—	—	—	—	1	3	—	3	1	4	3	4	2	3	3	1	6	3

<i>Harmothoe imbricata</i>	14	9	9	5	20	27	40	33	1	33	83	18	48	56	75	73	1	50	1	32
<i>Harmothoe impar</i>	—	—	3	4	20	26	15	34	—	—	—	114	217	252	273	271	—	187	73	86
<i>Pholoe minuta</i>	—	—	1	—	—	2	1	—	—	—	—	1	2	1	1	—	—	1	—	—
<i>Phyllodoce maculata</i>	—	—	—	1	—	1	—	—	—	—	1	—	6	9	3	2	—	—	1	—
<i>Eulalia viridis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eulalia sanguinea</i>	—	1	2	1	1	1	—	—	—	—	1	—	2	—	3	2	—	—	—	—
<i>Eteone picta</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Exogone gemmifera</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aulolytus avaticus</i>	3	14	30	16	12	8	15	12	—	—	6	13	12	11	7	12	10	6	18	5
<i>Nereis succinea</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	4	2	1	8	3
<i>Platynereis Dumerilii</i>	—	—	—	—	—	—	—	—	—	—	—	20	20	3	12	11	9	7	4	3
<i>Polydora ciliata</i>	3	2	4	10	5	7	11	11	—	—	4	20	20	19	12	—	—	—	—	—
<i>Arenicola marine</i>	1	1	3	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Amphitrite Johnstoni</i>	—	—	—	—	—	1	1	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Lanice conchilega</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Loxococoncha impressa</i>	—	+	—	—	—	—	+	—	—	—	+	+	++	++	++	++	++	++	++	+
Harpacticida:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Longipedia minor</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cirripedia:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Balanus crenatus</i>	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cunacra:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bodotritia scorpioides</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Corophium achenusicum</i>	—	—	—	—	1	1	1	—	—	—	2	3	3	2	6	6	7	4	1	4
<i>Microdeutopsis gryllotalpa</i>	—	—	—	—	—	—	—	1	—	—	—	—	1	—	2	—	—	3	—	3
<i>Caprella linearis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Decapoda:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Porcellana longicornis</i>	—	—	—	1	—	1	1	—	—	—	1	—	—	—	1	3	2	—	3	2
<i>Carcinides maenas</i>	—	—	1	1	—	—	1	2	—	—	1	—	4	2	1	1	—	—	—	—
Acari:	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Copidognathus fabrizius</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pycnogonida:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pallene brevistris</i>	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Anoplodactylus petiolatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mollusca:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrobia ulvae</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bryozoa:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bugula plumosa</i>	+	+	—	—	—	+	+	—	—	—	+	+	+	—	+	+	—	+	+	+
<i>Barentsia gracilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Yerseke, "Kijk-uit", 1943. Epifauna of samples of 25 oysters, born in 1941, and kept on trays. Oysters kept on trays at Yerseke in 1942, from 28/5 to 12/16 Winter 1942-1943 in basin at Bergen op Zoom. Replaced at Yerseke 28 5-1943. Supply exhausted 23-8-1943, after taking sample.

On 23 8 1943 oysters born in 1941, kept at Yerseke in 1942, and at Bergen op Zoom from 12-10-1942 to 23 8 1943, transferred to Yerseke, station „Kijk-uit“

Samples taken since 30 8 1943 from the latter oysters.

— absent, + present but rare, ++ moderate numbers, +++ abundant

Date	8/6	15/6	21/6	29/6	5/7	14/7	20/7	27/7	2/8	23/8	30,8	6/9	13/9	20/9	27/9	6/10
Water temperature °C	15.1°	16.8°	17.2	17.6°	18.2°	17.4°	19.2°	19.4°	21.5°	19.7°	17.5°	17.6°	18.0°	16.0°	13.7°	13.7°
Specific weight 17½° C	1.0215	1.0220	1.0215	1.0215	1.0225	1.0225	1.0235	1.0235	1.0215	1.0230	1.0225	1.0230	1.0230	1.0230	1.0235	1.0235
Area of shell surface per oyster (cm²)	± 40															± 60
Foraminifera:																
<i>Grithionina heinckei</i>	+	++	+	+	++	++	+	+++	+++	++	+	++	++	++	++	++
Ciliata:																
<i>Folliculina anphulla</i>	—	—	—	—	++	++	+++	+++	+++	+++	+++	+	++	+++	+++	+++
Porifera:																
<i>Sycon ciliatum</i>	—	—	—	—	—	+	+	+	+	++	—	—	—	—	+	—
<i>Haliclone limbata</i>	—	—	—	—	+	+	+	+	++	++	—	—	—	—	—	—
Coelenterata:																
<i>Laomedea loveni</i>	—	—	+	+	—	+	—	—	+	—	—	—	—	—	—	—
<i>Awella awella</i>	—	—	—	—	++	++	+++	+++	+++	+++	—	—	—	—	+	+
<i>Sagartia anguicomma</i>	—	+	—	—	—	—	—	—	+	—	—	—	—	—	—	—
<i>Diadumene cincta</i>	—	+	—	+	+	+	—	+	+	++	—	—	—	+	—	+
Nemertini:																
<i>Lineus ruber</i>	—	—	2	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Tetrahstemma flavidum</i>	—	—	—	—	2	—	—	—	—	—	1	—	1	—	1	—
Nematoda:																
<i>Eocephalus communis</i>	—	—	2 (juv.)	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Synplacostoma longicollis</i>	—	—	1 ♀	—	—	—	—	—	—	—	—	—	—	—	—	—
Polychaeta:																
<i>Lepidonotus squamatus</i>	—	—	—	1	3	4	5	3	8	10	—	—	1	—	—	2
<i>Harmothoe imbricata</i>	—	1	—	—	—	—	1	—	—	—	—	—	1	—	—	1
<i>Harmothoe impar</i>	18	7	32	17	68	81	69	68	64	58	10	58	87	80	67	91
<i>Pholoe minuta</i>	3	1	11	23	39	72	47	62	72	277	11	27	57	59	68	33
<i>Phyllodoce maculata</i>	2	1	5	2	1	4	—	3	1	1	—	—	1	—	—	1

<i>Eutalia viridis</i>	—	1 (juv.)	—	1	7	8	—	8	—	4	1	—	—	5	—	3	—	2	—	—	1	2
<i>Eutalia sanguinea</i>	7 (juv.)	1 (juv.)	2 (juv.)	3 (juv.)	1	—	—	—	—	—	1	16	—	—	—	—	—	2	—	—	1	1
<i>Etone picta</i>	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Mogalia peramata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Autolytus conulus</i>	—	1	7	2	—	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—
<i>Autolytus aurantiacus</i>	2	7	45	28	23	22	13	9	—	—	—	14	—	—	—	5	7	—	—	—	17	16
<i>Nereis succinea</i>	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2	—	—	1	—
<i>Platynereis Dumerilii</i>	2	—	4	—	2	—	—	—	—	—	—	—	—	—	—	4	2	—	—	—	2	4
<i>Polydora ciliata</i>	25	22	35	19	11	16	11	5	—	—	9	10	—	16	17	19	18	9	—	—	9	11
<i>Arenicola marina</i>	—	2	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Janice conchilega</i>	—	1 (juv.)	1 (juv.)	1 (juv.)	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
<i>Spionobis Pagenstecheri</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oligochaeta:																						
<i>Pelosclex benedeni</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Paronais littoralis</i>	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda:																						
<i>Loxconcha impressa</i>	2	—	—	—	—	1	—	—	—	—	2	—	—	+	++	++	++	+	+	+	+	+
Harpacticida:																						
<i>Longipedia minor</i>	+	+	+	+	+	+	+	+	—	—	+	+	+	+	++	+	+	+	+	+	+	++
Cumacea:																						
<i>Badotia scorpoides</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	1	1	—	2	2	—	—	2	4
Amphipoda:																						
<i>Corophium acherusicum</i>	—	—	1	2	1	3	—	—	—	—	4	9	—	—	3	10	18	13	—	—	13	12
<i>Micodotopsis gryllotalpa</i>	3	—	—	—	—	—	—	—	—	—	—	—	—	7	10	7	2	1	—	—	1	1
<i>Gammarus locusta</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	2	5	2	—	1	—	—	—	—
Decapoda:																						
<i>Porcellana longicornis</i>	—	—	—	1	2	1	2	1	—	—	9	3	—	1	3	6	3	—	—	—	—	4
<i>Carcinides maenas</i>	—	—	2	—	3	3	—	—	—	—	2	1	—	1	1	2	—	—	—	—	—	—
Pycnogonida:																						
<i>Pallene brevivestris</i>	—	—	—	—	3	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Bryozoa:																						
<i>Bugula plumosa</i>	+	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	+	++	—
Echinodermata:																						
<i>Ophiolithix fragilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Tunicata:																						
<i>Botryllus Schlozeri</i>	—	—	+	+	+	—	—	+	—	+	+	+	+	—	—	—	+	+	—	—	+	—

TABLE X

Yerseke, "Kijk-uit", 1944. Epifauna of samples of 50 oysters, born in 1943, and kept on trays.
Oysters placed at Yerseke 31-5-1944. Last sample 30-8 1944.

Due to war conditions sampling was impossible in September, October and November 1944.

— absent, + present but rare, ++ moderate numbers, +++ abundant

Date	5/6	22/6	28/6	5/7	13/7	19/7	26/7	2/8	9/8	16.8	23/8	30/8
Water temperature °C	15.3°	15.6°	16.9°	18.2°	17.6°	18.7°	19.1°	19.1°	20.5°	19.9°	21.3°	20.2°
Specific weight 17½° C	1.0215	1.0205	1.0210	1.0205	1.0205	1.0205	1.0205	1.0205	1.0201	1.0205	1.0205	1.0205
Area of shell surface per oyster (cm ²)	6	9	11	13	15	21	20	23	26	33	36	41
Foraminifera:												
<i>Grithionina heinckei</i>	—	—	+	+	+	+	+	+	+	+	+	+
Ciliata:												
<i>Folliculina ampulla</i>	—	+	+	+	+	++	++	+++	+++	+++	+++	+++
Porifera:												
<i>Sycon ciliatum</i>	—	—	—	—	—	—	—	+	+	+	+	++
<i>Haliclone limbata</i>	—	—	—	—	+	+	+	+	+	+	+(g)	+(g)
Coelenterata:												
<i>Aurelia aurita</i>	—	—	—	—	+	+	+	+	++	++	++	+
Nemertini:												
<i>Tetrastemma flavidum</i> . . .	—	1	—	—	—	—	—	—	—	—	—	—
<i>Nematoda</i>	—	—	+	—	+	+	+	+	+	+	+	+
Polychaeta:												
<i>Lepidonotus squamatus</i> . . .	—	—	—	—	—	4	2	4	2	2	1	2
<i>Harmothoe imbricata</i>	—	—	—	—	—	—	—	—	—	—	1	—
<i>Harmothoe impar</i>	1	4	6	9	6	11	7	19	23	28	27	30

[illegible]

Yerseke, "Kijk-uit", 1945. Epifauna of samples of 50 oysters, born in 1944, and kept on trays. Oysters placed at Yerseke 27 4-1945
 — absent, + present but rare, ++ moderate numbers, +++ abundant

Date	17/5	5/6	18/6	25/6	3/7	9/7	16/7	24/7	30/7	7/8	13/8	21.8	3.9
Water temperature °C	16.7°	15.9°	17.1°	19.5°	17.6°	19.1°	20.3°	20.4°	19.3°	19.2°	19.0°	17.4°	18.6°
Specific weight 17½° C	1.0200	1.0200	1.0200	1.0205	1.0200	1.0205	1.0210	1.0210	1.0215	1.0215	1.0215	1.0210	1.0215
Area of shell surface per oyster (cm ²)	7	8	12	16	19	17	22	26	30	32	34	36	47
Foraminifera:													
<i>Critinonina heinckei</i>	—	—	++	++	+++	+++	++	+++	+++	+++	++	+-	+
Ciliata:													
<i>Folliculina ampulla</i>	—	—	+	+	++	+++	+++	+++	+++	+++	+++	+++	+++
Porifera:													
<i>Haliclone limbat</i>	—	—	—	+	+	+	+	+	+	+	+	+	+
Coelenterata:													
<i>Aurelia aurita</i>	—	—	—	—	++	++	++	++	++	++	++	++	+
<i>Sagartia angulicoma</i>	—	—	1	—	—	1	4	—	1	1	1	1	2
<i>Diadumene cincta</i>	1	—	—	—	—	—	—	—	2	3	1	5	3
Nematoda:	—	—	—	+	—	+	+	—	+	—	+	—	—
Polychaeta:													
<i>Lepidonotus squamatus</i>	—	1	6	5	6	3	6	6	6	4	4	4	3
<i>Harmothoe imbricata</i>	—	—	1	1	2	1	—	—	—	—	1	—	—
<i>Harmothoe impar</i>	—	23	59	59	42	36	41	64	62	53	60	41	60
<i>Pholoe minuta</i>	—	1	1	26	44	35	56	68	95	90	125	120	175
<i>Phyllodoce maculata</i>	3	—	—	—	—	—	—	2	2	—	1	—	—

<i>Eulalia viridis</i>	—	—	3	3	1	5	5	5	2	3	2	9
<i>Eulalia sanguinea</i>	—	6	12	10	4	8	8	2	2	2	1	2
<i>Autolytus auantiacus</i>	6	7	26	17	14	5	37	9	9	5	15	11
<i>Platymereis Dumerilii</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>Polydora ciliata</i>	26	19	3	4	2	1	2	3	—	2	1	6
<i>Amphitrite Johnstoni</i>	—	1	—	—	—	—	—	—	—	—	—	—
Ostracoda:												
<i>Loxoconcha impressa</i>	—	—	—	—	—	—	+	+	—	—	—	—
Harpacticida:												
<i>Longipedia minor</i>	+	+	+	+	+	+	+	+	+	+	+	+
Cirripedia:												
<i>Balanus crenatus</i>	+	+	+	+	+	—	—	—	—	—	—	—
Amphipoda:												
<i>Corophium acherusicum</i>	—	—	—	—	—	—	—	—	1	1	—	1
Decapoda:												
<i>Carinides muenas</i>	—	—	1	—	—	1	—	2	—	2	1	—
Pycnogonida:	—	1	2	4	4	4	1	1	—	—	—	—
Mollusca:												
<i>Crepidula fornicata</i>	—	1	—	—	—	1	1	2	—	2	—	2
Bryozoa:												
<i>Bugula plumosa</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Barentsia gracilis</i>	—	—	+	—	—	—	—	—	—	—	—	—
Echinodermata:												
<i>Asterias rubens</i>	—	—	—	1 (juv.)	—	—	3 (juv.)	—	—	1 (juv.)	—	—

TABLE XIII

Water temperature (monthly and fortnightly averages, °C.)

	1940	1941	1942	1943	1944	1945	1921- 1939
January	-1.5	-0.9	0.3	2.9	4.5	0.9	3.1
February	-1.5	1.2	-1.5	3.0	3.6	3.7	3.0
March	3.7	4.7	0.9	6.4	3.5	7.4	4.9
April	8.6	7.4	8.2	10.7	9.5	11.2	8.5
May	14.8	10.8	11.7	14.0	12.6	14.0	13.3
June I	17.9	14.8	15.8	16.7	15.5	16.4	16.5
June II	17.7	19.6	16.9	17.2	16.1	18.5	17.3
July I	18.7	21.5	18.3	17.7	18.0	18.6	18.7
July II	18.1	20.3	17.2	19.8	18.7	20.1	19.5
August I	18.7	17.8	18.1	19.3	20.1	18.9	19.1
August II	16.8	16.8	19.9	18.6	20.8	18.1	18.5
September I	15.6	17.3	19.5	17.6	15.4	18.2	17.7
September II	14.0	16.8	15.8	15.7	14.8	16.4	15.6
October	9.2	13.1	13.4	13.1	11.9	13.7	12.1
November	7.7	6.2	8.6	8.0	7.2	8.5	7.1
December	3.3	5.5	5.6	3.1	4.5	4.4	3.4

TABLE XIV

Monthly averages specific weight 17½ °C.

	1940	1941	1942	1943	1944	1945	1921- 1939
January	—	1.0200	1.0200	1.0205	1.0215	1.0175	1.0209
February	—	1.0185	—	1.0200	1.0215	1.0175	1.0206
March	1.0190	1.0190	1.0200	1.0215	1.0195	1.0185	1.0207
April	1.0185	1.0190	1.0195	1.0215	1.0195	1.0190	1.0208
May	1.0190	1.0200	1.0200	1.0220	1.0200	1.0195	1.0209
June	1.0200	1.0200	1.0215	1.0220	1.0205	1.0200	1.0211
July	1.0205	1.0205	1.0210	1.0235	1.0200	1.0215	1.0214
August	1.0210	1.0205	1.0215	1.0230	1.0205	1.0210	1.0218
September	1.0205	1.0205	1.0210	1.0230	1.0200	1.0225	1.0218
October	1.0200	1.0210	1.0200	1.0220	1.0190	1.0215	1.0218
November	1.0195	1.0205	1.0215	1.0220	1.0185	1.0205	1.0214
December	1.0200	1.0200	1.0215	1.0220	1.0185	1.0200	1.0213

Epifauna of miscellaneous oyster samples. Oysters partly from trays, partly from oyster plots. Samples of preliminary investigations included



SCHOUWEN - DUIVELAND

NOORD BRABANT

THOLEN

ZUID BEVELAND

OOSTER -
SCHELDE
SCHAAL

0 1 2 KM

QUANTITIES OF WATER PUMPED
BY MUSSELS (*MYTILUS EDULIS*) AND
COCKLES (*CARDIUM EDULE*)

by

J. WILLEMSSEN

(*Zoological Station, Den Helder*)

I. INTRODUCTION

From the viewpoint of feeding and respiration of the animals themselves and also from that of water purification it is of importance to know the quantities of water pumped by bivalve molluscs. They have been measured for oysters and mussels. In connection with other investigations carried out by the Zoological Station it was of interest to determine them also for the cockle. This paper gives the results of some measurements for the latter, together with new figures for the mussel.

The quantity of water pumped has been determined for bivalves in two ways:

1. after a direct method, whereby the water from the exhalation siphon was collected and its volume measured;
2. according to an indirect method, whereby the animals were given the opportunity to clear suspensions, and the decrease in suspended matter was used to calculate the volume of water pumped.

It should at once be added that the direct method in the hands of such investigators as GALTISOFF c.s. and LOOSANOFF and co-workers is able to give constant figures even over rather long periods of time, whereas the indirect method up till now gave figures which are little constant and possibly less reliable. Because all direct determinations refer to the oyster and all indirect ones to the mussel, however, it is possible that the different results are due to the different behaviour of these species. I return to this point further on.

Up till now the following results have been obtained:

<i>Ostrea virginica</i>	Maximum quantity pumped	GALTSOFF (1928)
" "	3.9 litres per hour	
" "	5-16 litres per hour	GALTSOFF, CHIPMAN, ENGLE and CALDERWOOD (1947)
" "	12.5-18, maximum	LOOSANOFF and NOMEJKO
" "	31-34 litres per hour	(1946)
" "	Maximum (under abnormal circumstances) 26 litres per hour	LOOSANOFF and ENGLE (1947)
<i>Mytilus californianus</i>	Average 2.6, extremes 0.5 and 18.1 litres per hour	FOX, SVERDRUP and CUN- NINGHAM (1937)
<i>Mytilus edulis</i>	0.7 litres (animals of 5 grams weight of flesh)	VON HARANGHY (1942) ¹
" "	Average 0.43, maximum 1.3 litres (animals of 15-32 mm)	BARKER JØRGENSEN (1949)

The first four references refer to direct, the last three to indirect measurements. Especially valuable are the results published by GALTSOFF c.s. (1947), LOOSANOFF and NOMEJKO (1946), and LOOSANOFF and ENGLE (1947).

DODGSON (1928) found for *Mytilus edulis* volumes pumped of 2 litres per hour, but he neglected the fact that the same water was pumped by his animals more than once. He was of opinion that the quantity of material kept back was directly proportional to the quantity of water pumped, whereas in reality this relation is not linear, but logarithmic, so that his values became too low. On the other hand, he neglected the fact that the suspended material partly sinks, which made his figures too high.

II. METHODS

The method used by me was the indirect one, worked out by Fox, SVERDRUP and CUNNINGHAM (1937); it was used in a simplified form, however. The property of bivalves to sieve suspended particles from the water is here made the starting point. This property does not only concern plankton and silt, but also bacteria (ZOBELL and FELTHAM, 1938) and even colloids (DAMAS, 1935; Fox and COE, 1943, p. 226). The material is kept back on the gills and partly ingested, partly refused and given off as pseudofeces.

¹ VON HARANGHY does not mention the volumes here given, but I have calculated them from his figures. At 20° C the turbidity within 30 seconds decreases from 100 to 50 % in a vessel of 500 cc. The volume pumped is then $500 \ln \frac{100}{50} = 0.7$ litres per hour (see below).

A. EXPERIMENTS WITH MUSSELS

When starting the work with mussels suspensions of carmine and Chinese ink were used. They are not very suitable, as they partly dissolve so that the current leaving the exhalation siphon is still coloured. This is not the case if fine silt is used. If a concentrated suspension of silt is brought into the inhalation siphon the outgoing current remains perfectly clear. Apparently, the silt is wholly sieved from the water.¹

Suspensions for the experiments with mussels were made of silt particles smaller than $60\ \mu$. These were obtained by passing silt from the sea through a fine meshed plankton net. The silt in question consists of organic detritus, clay and fine sand.

The mussel was placed in a glass cylinder of 600–1000 cc and care was taken that it attached itself to the wall, so that the bottom remained free.

The silt content in the glass under such conditions decreases due to two causes. Part of the silt sinks to the bottom, part of it is taken in by the animal together with the water, and retained. In order to reduce sinking to a minimum the water was kept in motion by bubbling air through it. This had the advantage that it was constantly saturated with oxygen, so that the animals were not in need of pumping faster because of oxygen shortage. Since the mussel was not allowed to fix itself on the bottom the circulating water could easily bring the silt from there in suspension again.

The temperature was kept low by placing glass and tubes in water being regularly refreshed.

To obtain exact figures for the quantity of water the mussels got at their disposal the glass and mussel were well emptied before filling. This was done by placing glass and mussel upside down, so that the animal too lost all the water contained within its mantle cavity.

At least half an hour after the mussel had well opened its siphons the silt was added by emptying a 5 or 10 cc pipette above the rising air bubbles. In this way the silt was at once divided through the circulating water.

The current velocity of the pumping mussels was calculated after the method used by FOX, SVERDRUP and CUNNINGHAM (1937).

When the volume of the glass is m and the silt concentration at the time t is c_t , the quantity of silt sinking down per second amounts to

¹ FOX, SVERDRUP and CUNNINGHAM have shown that all the material from the water passing the gills may indeed be kept back. As one cannot be sure, however, that the material is always fully retained the volumes found should be considered minima.

$a \cdot c_t \cdot m$, a representing a proportion factor. In the time dt the quantity sinking is then $dt \cdot a \cdot c_t \cdot m$.

If the animal pumps x cc water per second and would keep back all the silt contained in it $x \cdot c_t$ cc of silt are retained per second, or $dt \cdot x \cdot c_t$ cc in the time dt .

The change in silt content, $d(c_t m)$, is given by the material deposited and the material kept back by the molluscs. This change is negative:

$$d(c_t m) = - (dt \cdot a \cdot c_t \cdot m + dt \cdot x \cdot c_t)$$

$$\frac{dc_t}{c_t} = - dt \left(a + \frac{x}{m} \right)$$

Integrating this one finds:

$$\ln c_t = - \left(a + \frac{x}{m} \right) t + C, \text{ in which } C \text{ is a constant.}$$

For $t = 0$ this formula reads:

$$\ln c_0 = C, \text{ so that } \ln c_t = - \left(a + \frac{x}{m} \right) t + \ln c_0$$

$$\text{It follows from this that } x = m \left(\frac{\ln c_0 - \ln c_t}{t} - a \right).$$

Of these factors, m , c_0 , c_t and t , differing under different conditions, can easily be determined, whereas the determination of a may take place in the following manner. When no animal is present $x = 0$, so that $x = m \left(\frac{\ln c_0 - \ln c_t}{t} - a \right)$. As m cannot be zero $\frac{\ln c_0 - \ln c_t}{t} - a = 0$.

This means that $a = \frac{\ln c_0 - \ln c_t}{t}$. As c_0 , c_t and t are known a may be calculated. It depends among others on the form of the glass and the animals and was for each separate animal calculated from two or three measurements.

c_0 and c_t , the concentrations at the beginning and the end of the experiment, were measured by filtering a certain quantity of the water (5–10 cc in the case of c_0 , some hundreds of cc in the case of c_t), and weighing the filter paper after drying at 120°C . Only the beginning and end concentrations were determined, whereas FOX, SVERDRUP and CUNNINGHAM measured the concentration every 5 minutes. My results are therefore in this respect less exact than theirs.

B. EXPERIMENTS WITH COCKLES

In the experiments with cockles the Protozoan *Noctiluca miliaris* was used instead of silt. This species in the beginning of July was quite numerous near the Zoological Station, especially at high tide. The cockles took them in readily, but I do not know whether they were also

ingested. The specific weight of *Noctiluca* is somewhat lower than that of seawater, so that they do not sink to the bottom and one needs not reckon with such sinking. They were well dispersed by the circulating water and the concentration can easily be determined by filtering them off on a black filterpaper and counting them.

In most experiments 4 cockles were placed in a cylinder glass of 255 cc and the concentration was determined every 5 minutes for a period of 15–20 minutes. Each value for the quantity of water pumped is the mean of 3–4 figures obtained in one such series.

To get an idea of the degree of exactness in measuring the concentration the latter was determined 7 times in a *Noctiluca*-suspension without cockles. Their average number was 87 specimens per 10 cc with a mean error of 6%.

III. RESULTS

The results for the mussel are given in table I.

TABLE I

Mussel	Length in mm	Breadth in mm	Quantity of water pumped in litres per hour	Maximum
A	68	30	1.9	3.2
B	68	30	3.2–1.9–1.9–0.7	
C	77	33	2.3	
D	80	32	1.0–0.4–0.2	
E	67	29	1.8–2.6–0.9–1.3	2.6
			1.1–1.9–1.2	
F	81	38	3.2–1.8–4.6–3.7–	4.6
			1.7–0.9	
G	48	25	1.4–0.8–1.1–1.3–0.7	1.4

The average for 27 observations is 1.7 litres per hour, the maximum for a large animal (at least for a short period) is 4.6 litres per hour. The water temperature during the experiments was 11.8–14.7° C.

It was stated above already that the indirect method is only able to give minimum values. One might therefore be inclined to suppose that the maximum values found represent the right ones and that all the others are too low. This seems also possible from the fact that there is so much variation for one and the same animal within a short period of time. If the results found after the indirect method for the mussel are compared with the certainly quite reliable values for the oyster found with the direct method by GALTISOFF, CHIPMAN, ENGLE and CALDERWOOD and by LOOSANOFF, NOMEJKO and ENGLE it attracts attention that the oyster may furnish relatively quite constant values for long

periods at a time. It seems, nevertheless, not impossible that these variations in the mussel do not represent abnormalities. First of all, the oyster too may sometimes show abnormally high values, which occur when clear water is available after the animals have been in "dirty" water for some time. LOOSANOFF and NOMEJKO found for some animals average values as high as 25-27, and a maximum of 31-34 litres per hour. Secondly, there is a direct connection in my experiments between the size of the mussels and the average pumping velocity, and this is in favour of normal behaviour. The large animals C, D, F (77-80 mm long) show an average of 1.9, the animals A, B, E (67-68 mm) an average of 1.7 and the animal G (48 mm) an average of 1.1 litres per hour. This may mean that the volumes pumped are true. Generally speaking, the mussel lives in much more silty water than the oyster, and its pumping behaviour may accordingly differ and show much variation from one moment to another. It is probable from VAN DAM's observations on *Mya arenaria* (1937, p. 90) that pumping is faster shortly after a period of oxygen shortage than some time later. It would be worth while to try and gather pumping figures for the mussel by way of the direct method in order to get certainty on this point. As long as such figures are wanting we do probably best to assume that large *Mytilus edulis* of 70-80 mm length have an average pumping rate of 1.8 litres an hour, whereas smaller mussels pump accordingly less.

The temperatures used in my experiments (11.8-14.7° C) differed too little to prove the existence of a connection between temperature and current velocity. Such a connection has been shown to exist in the oyster (GALTISOFF, 1928).

The results for the cockle are given in table II.

TABLE II

Number of animals	Length and breadth in mm	Quantity of water pumped per cockle in litres per hour
4		0.3
4		0.6
3	39/34, 37/31, 40/33	0.7
4	30/26, 26/23, 30/28, 32/28	0.2
4	34/29, 37/31, 30/25, 31/26	0.3
1	39/34	1.1
4	22/19, 29/24, 33/26, 28/25	0.7
1	39/34	2.5

It was stated already that each value represents the mean for 3-4 ones obtained separately, the total number of measurements is therefore again about 27.

The average for all values is 0.56 litres per cockle per hour. If the exceptionally high value of 2.5 litres is omitted the average is 0.48. We therefore may assume that adult animals pump about 0.5 litres per hour. The temperature of the water during the experiments was 17.3–19.5° C.

IV. SUMMARY

The average quantity of water pumped by mussels (*Mytilus edulis*) of 70–80 mm long probably amounts to 1.8 litres per mussel per hour at temperatures of 11.8–14.7° C; smaller mussels pump less. The maximum found for a large mussel was 4.6 litres.

The average quantity pumped by cockles (*Cardium edule*) of some 30–40 mm length amounts to 0.5 litres per cockle per hour at 17.3–19.5° C; the maximum found was 2.5 litres.

It is probable that these values are more or less right, but the determination of the pumping rate after a direct method would be valuable.

I am much indebted to Dr J. VERWEY for his helpful suggestions, his thorough criticism and particularly for translating the manuscript.

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THE PREFERENCE OF THE SLUG *AEOLIDIA*
PAPILLOSA (L.) FOR THE SEA ANEMONE
METRIDIUM *SENILE* (L.)

by

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(Zoological Station, Den Helder)

I. INTRODUCTION

It is a well known fact that most of the nudibranchiate sea slugs use coelenterates as food. It also holds for one of the commonest species of the Dutch coast, *Aeolidia papillosa*, which feeds on the sea anemone *Metridium senile*.

Looking more closely at the relation *Aeolidia-Metridium* it is natural to ask: Does *Aeolidia* indeed prefer *Metridium*? If so, on what is this preference based? How does *Aeolidia* discern *Metridium* from other sea anemones? If it finds its food by scent, does *Metridium* give off a different scent from *Actinothoe* or other species?

During a stay at the Zoological Station, Den Helder, in the summer and autumn of 1949 I tried to give an answer to these questions. It should at once be stated that the answer obtained was only a partial one.¹

II. METHODS

After a number of preliminary experiments the following method was used to see if *Aeolidia* could find sea anemones from some distance and whether it reacted differently on different species.

A number of *Aeolidia papillosa* were brought into an aquarium (fig. 1), receiving its water through two glass siphons from two small aquaria placed at a somewhat higher level. The siphons were chosen so wide that the slugs, if necessary, could pass them. One leg stood vertically in the small, the other slopingly on the bottom of the larger aquarium,

¹ Study of the subject was suggested to me by Dr J. VERWEY, Director of the Station; literature directly bearing on it was not found.

where both siphons were placed in each other's immediate neighbourhood. The water level in the small aquaria was kept constant through overflow, whereas the difference in water level between small and large aquaria, which determined the current velocity in the siphon, was regulated through a second siphon in the large aquarium, functioning at the same time as outflow of the latter.

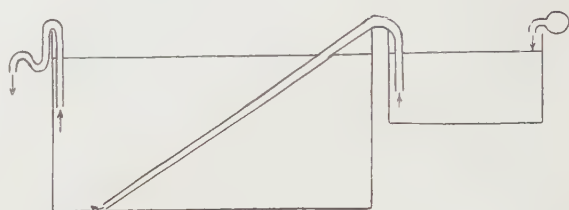
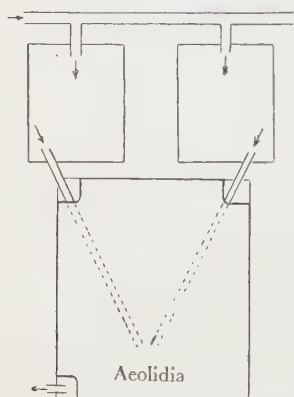


Fig. 1

There were a number of such sets of three aquaria and in each large aquarium a number of *Aeolidia* were placed, whereas actinians were placed into one of the small aquaria of each set. The second small aquarium of each set contained water only. – The large aquarium with slugs was closed by a glass plate in order to prevent the animals from leaving it; *Aeolidia* is often inclined to leave the water, not only in aquaria, but also in nature.

It was hoped that *Aeolidia*, should it scent the anemones, might concentrate around the lower end of the siphon leading to the aquarium with anemones and perhaps even enter it; there was no concentration difference in the siphon itself, however.

The first experiment was carried out with 10 *Aeolidia*. The anemone used was *Metridium*. Within 25 minutes 8 of the 10 slugs had entered the siphon, crept through it and reached the anemones. None of them entered the other siphon. In a second experiment the slugs collected around the siphon entrance leading to the anemones without entering it. It appeared that the current was too strong, the animals entering immediately after the current velocity had been lowered. It resulted from these experiments that the level difference between the small and the large aquaria had to be quite small and as this could easily be changed via the length of the outflow-siphon in the large aquarium regulation of the current velocity gave no difficulty.

The following experiments were all carried out after the same method in 4 (later 6) sets of 3 aquaria each.

They represented 3 series:

- I, in which different species of sea anemones were tested against sea water without anemones;
- II, in which different species of sea anemones were tested against each other;
- III, in which young *Metridium* were tested against old ones; damaged anemones against undamaged ones; contracted anemones against expanded ones.

In the first series 9-12 slugs were used in each set of 3 aquaria, in the second and third series 20. - When *Aeolidia* grew older the siphon diameter had to be taken wider in order to make passage of the animals possible and the glass siphons were therefore exchanged for wide celluloid ones, which functioned quite as well.

In the last series of experiments care was taken to maintain a certain difference in scent concentration between small and large aquaria by way of a separate inflow of sea water into the large aquarium. This was necessary, because without the latter the animals apparently had difficulty in perceiving differences. Such a separate inflow of sea water into the large aquarium should also have been used in the experiments of Series II, but this was realized only afterwards, when the experiments had been finished. It is possible that the use of an extra-inflow would even have been advantageous in the experiments of the first series.

III. RESULTS

In the first series of experiments 4 species of sea anemones were tested against blanks. This means that *Aeolidia* had to choose between a current of sea water from the general water circulation of the Station and a similar current which had passed an aquarium with anemones. The four species of anemones in question were *Metridium senile* (L.), *Diadumene cincta* STEPHENSON, *Actinothoe anguicoma* (PRICE)¹ and *Tealia felina* (L.). Some few individuals (of *Tealia* only one) were used in each case. One should well realize that the only difference between both media presented to the slugs was that one of them had been in contact with sea anemones just before, the other not. If, therefore, the results would show that the water which had flown over the anemones is clearly preferred, this would mean that in the sea too *Aeolidia* may be directed by this same influence and find its anemones from some distance.

¹ The possibility is perhaps not to be excluded that also *Sagartia troglodytes* (PRICE) has been among the specimens tested. The species resembles *Actinothoe anguicoma* (PRICE). See also Postscript.

Each experiment took about 24 hours and the number of slugs in each of the 4 sets of 3 aquaria was 9-12. The number of *Aeolidia* tested per experiment was therefore 36-48. As the number of experiments was 14 the data have been obtained from some 600 separate observations.

It results from table I that in 14 experiments with 9-12 slugs 52 % of the slugs reach *Metridium senile*, none the water without anemones; of the same number tested 14 % reach *Diadumene cincta*, 1 % the water without anemones; of the third set 9 % reach *Actinothoe anguicoma*, none the water without; of the fourth set 8 % reach *Tealia felina*, 1-2 % the water without.

It is clear from these data that *Aeolidia papillosa* can easily discern between water which shortly before has passed anemones from water which has not. There is no doubt, therefore, that *Aeolidia* must be able to find its anemones from some distance also in the sea.

Secondly, it is clear that *Aeolidia* is much more strongly attracted to *Metridium senile* than to *Diadumene cincta*, *Actinothoe anguicoma* and *Tealia felina*, for *Metridium* catches 52 % of the slugs tested, the other species only 14, 9 and 8 % respectively.

The following series of experiments was made to get further proof about this relation between *Metridium* and the other species. The four species of sea anemones were now tested against each other, i.e., the slugs got to choose between a current of sea water that had passed one species and a current that had passed another. Each experiment took about 20 hours and there were 14 experiments in all. There were 6 sets of 3 aquaria now. The number of slugs in each of the sets was 20, the total series referred to some 1400 separate observations.

Table II gives the results. The figures are less convincing than one would have expected and this is certainly due to several causes. First of all, there was less concentration difference between the large aquarium and the small ones than in the experiments of series I, since the small aquaria feeding the large one both contained anemones now. The concentration difference between large and small aquaria must therefore soon have decreased, a possibility which was only realized after the experiments had been finished. This may be the reason why the percentages of slugs reaching *Metridium* were so much smaller than in the experiments of series I. Secondly, the activity of *Aeolidia* decreases with increase of age. Thirdly, the experiments of series a and b (table II) from 7 and 8 November onward gave me the impression that closed *Metridium* do not attract slugs as do open anemones. It further occurred several times that *Actinothoe* had somewhat been damaged on collecting (20 October, 7 November, see table II) and such specimens were apparently more attractive than normal ones. Similarly, *Metridium* was damaged after the slugs had reached and fed on them and they worked

TABLE I

Percentages of *Aeolidia* attracted by different species of sea anemones, tested against water without anemones. The figures represent percentages of the total number of *Aeolidia* used in each experiment (9-12 specimens). For further explanation see text

	24/9	26/9	27/9	28/9	29/9	30/9	3/10	4/10	5/10	6/10	7/10	8/10	9/10	10/10	Average
A. <i>Metridium</i> . . .	10	100	44	91	45	63	81	20	10	100	100	32	13	15	52%
Water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0%
B. <i>Diadumene</i> . . .	10	0	76	33	0	50	10	0	10	0	0	0	10	0	14%
Water	0	0	0	10	0	0	0	0	0	0	0	0	0	0	1%
C. <i>Actinothoe</i> . . .	0	0	44	8	9	0	9	25	0	22	0	5	0	0	9%
Water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0%
D. <i>Tealia</i>	10	0	0	10	0	10	10	0	0	0	22	16	21	14	8%
Water	0	0	0	0	0	0	0	0	10	0	11	0	0	0	1-2%

TABLE II

Percentages of *Aeolidia* attracted by different species of sea anemones, tested against each other. The figures represent percentages of the total number of *Aeolidia* used in each experiment (20 animals). For further explanation see text

	12/10	13/10	14/10	15/10	18/10	19/10	20/10	21/10	7/11	8/11	9/11	10/11	11/11	12/11	Average
A. <i>Metridium</i> . . .	20	0	0	25	30	25	5	5	0	0	0	0	0	0	8%
<i>Tealia</i>	5	0	5	0	100	5	5	15	5	5	0	0	0	0	2.5%
B. <i>Metridium</i> . . .	40	20	5	70	0	0	15	15	10	0	0	0	0	0	20%
<i>Actinothoe</i>	0	0	0	0	0	5	40	15	30	10	20	10	5	10	10%
C. <i>Metridium</i> . . .	0	5	10	0	85	10	60	60	10	0	5	65	0	15	25%
<i>Diadumene</i>	0	10	0	5	0	0	0	0	5	0	0	0	5	5	2%
D. <i>Tealia</i>	0	0	0	0	0	0	10	0	20	0	0	0	5	0	3%
<i>Actinothoe</i>	0	20	45	0	5	5	5	5	5	5	5	15	0	5	10%
E. <i>Tealia</i>	0	10	0	0	0	0	10	15	0	0	10	15	10	15	7%
<i>Diadumene</i>	0	15	0	0	0	0	0	0	0	0	15	0	0	5	3%
F. <i>Actinothoe</i> . . .	0	0	0	0	0	0	0	0	10	0	10	0	5	10	6%
<i>Diadumene</i>	0	0	0	0	0	0	0	0	20	0	0	5	20	5	12%

strongly attractive then, one of them attracting 12 slugs on 20 as well as 21 October. This means that, also in undamaged specimens, besides quality also quantity of scent might play a role. *Metridium*, for instance, with its rich production of mucus, might give off more scent than *Diadumene*. There is the more reason to believe so, because *Metridium* does, in fact, give off a rather strong smell, which is easily perceived also by us. One should therefore at least try to work with comparable scent-emitting surfaces (assuming that the surface in this connection is important). This, however, is very difficult, especially so in the case of *Diadumene cincta*, which is quite small and which was preferentially used in small numbers, since it does not easily attach itself to the glass and is therefore easily carried away by the water current.

Notwithstanding these difficulties the results more or less corroborate those of the first series of experiments.

Metridium is preferred when compared with *Tealia felina*, *Actinothoe anguicoma* and *Diadumene cincta*, whereas there is no clear preference when the last 3 species are mutually compared; taking the results of both series of experiments (I and II) together one is inclined to suppose that *Diadumene* after *Metridium* comes first, *Actinothoe* and *Tealia* last, but series E (table II) does not support that supposition (compare also p. 169).

The fact that *Aeolidia papillosa* clearly prefers *Metridium senile* when compared with the other species of sea anemones tested may, as already stated, be due to two causes. Assuming that chemoperception plays a role here, the first possibility is that the different species of anemones give off a different scent and that *Aeolida papillosa* is especially attracted by the scent of *Metridium* because of its special character. The second possibility is that all these anemones give off a similar scent, and that *Aeolidia* is attracted strongest by that species that gives off the strongest scent.

In view of the fact that *Aeolidia papillosa* first and foremost feeds on *Metridium senile* (and, according to other observations, also on *Actinia equina* L.), when these under aquarium conditions are presented together with *Diadumene cincta*, *Actinothoe anguicoma* or *Tealia felina*, one is inclined to assume that nature uses different scents as a base for the mutual relation between the slugs and the anemones. For a *Tealia* close by will always scent stronger than a *Metridium* far off and this would lead to the attack of *Tealia*, if strength of scent would play a role; nevertheless, in an aquarium, where all anemones at one moment or the other are close by, *Metridium* is strongly preferred.

There are, however, some facts, which point to the possibility that strength of scent is, to say the least, not negligible. It was stated above already that damaged and possibly also open anemones attracted more

slugs than undamaged and closed ones. If damaged *Actinothoe*, however, would attract more slugs than undamaged *Metridium* (20 October and 7 November, table II), this would be in favour of the supposition that strength of scent is also of influence. It should at once be added that this question was not definitely solved, because the time at my disposal was used up in the experiments of series VI mentioned before.

If, namely, one wants to compare damaged *Actinothoe* and undamaged *Metridium* one should first of all be acquainted with the influence of damage as such, studied in one single species. Damaged and undamaged *Metridium* were therefore compared first. As the foregoing experiments, however, had furnished indications, that also closed and expanded *Metridium* might have a different influence on *Aeolidia* such animals were compared at the same time. There were moreover indications of a different influence of young and old anemones and these were therefore tested too. The whole third series of experiments therefore referred to one and the same species: *Metridium senile*. After it had been finished time was up and the comparison of damaged and undamaged specimens of different species had to be omitted.

The single experiments of series III lasted about 12 hours and 20 slugs were used in each of them, except in those of 10 December, in which the number was 16. The quantities of anemones were taken more or less comparable as to volume. It was already remarked that the large aquaria got extra-water to maintain a concentration difference between large and small ones.

TABLE IIIa

Percentages of *Aeolidia* attracted by young and old, damaged and undamaged, and expanded and contracted *Metridium*. No coating of cotton-wool around end of siphon

<i>Metridium</i>	10/12	11/12	12/12	13/12	14/12	Averages
a. young	31	10	85	35	20	36 %
b. old	0	15	0	10	5	6 %
a. damaged . . .	18	35	35	15	25	26 %
b. undamaged . .	6	10	10	15	15	11 %
a. expanded . . .	12	10	45	20	30	23 %
b. contracted . .	6	20	5	10	20	12 %

The results are given in table IIIa. In 5 experiments an average of 36 % of the slugs chose young, only 6 % old *Metridium*; 26 % chose wounded against 11 % undamaged anemones; 23 % chose expanded against 12 % closed *Metridium*. It seems clear that *Metridium* attracts more slugs when it is young, damaged and expanded than when the contrary is the case. One is inclined to assume that in all these cases

strength of scent causes the differences in question. This would mean that young and also expanded *Metridium* give off more scent than old, respectively contracted ones. At any event, this would hold in the first mentioned case.

During these experiments the following difficulty arose, however.

When undamaged *Metridium* attracted *Aeolidia* they thereafter acted as damaged ones and the percentage of slugs attracted became higher than was to be expected from undamaged anemones. Therefore, in another series of experiments the siphon ends in all aquaria with undamaged anemones (all aquaria except that containing the wounded animals in series b) got a coating of cotton-wool tied around them.

TABLE IIIb

Percentages as in table IIIa. With coating of cotton-wool around end of siphon

<i>Metridium</i>	15/12	15/12	16/12	16/12	17/12	17/12	18/12	18/12	19/12	19/12	Average
a. young	30	0	5	0	15	20	25	20	10	25	15.0 %
b. old	5	0	0	0	15	0	30	15	0	0	6.5 %
a. damaged	30	30	65	30	10	15	40	55	25	10	31.0 %
b. undamaged	0	10	0	0	5	0	0	0	5	5	2.5 %
a. expanded	30	20	0	5	10	10	20	5	5	10	11.5 %
b. contracted	20	5	0	0	10	5	20	30	10	5	10.5 %

The results are given in table IIIb whereas in table IV the results of table IIIa and IIIb are compared.

TABLE IV

Percentages of IIIa and IIIb compared

	Averages table IIIa	Averages table IIIb
a. young	36 %	15.0 %
adult	6 %	6.5 %
b. wounded	26 %	31.0 %
not wounded	11 %	2.5 %
c. contracted	12 %	10.5 %
expanded	23 %	11.5 %

Table IV makes it probable that young *Metridium senile* indeed attract more slugs than old individuals. The great difference between the results of series IIIa and IIIb may be due to the fact that young animals in series IIIa, which had been damaged by *Aeolidia*, got too high a percentage of slugs through the damage done.

Further, wounded anemones attract more slugs than undamaged ones. — Thirdly, it is uncertain whether there really is a difference between expanded and contracted animals, the two cotton-wool series giving a difference that is negligible; the influence of damage done by entering slugs may have played a rôle in series IIIa here.¹

These experiments with sieves of cotton-wool are also of interest from another point of view. Up till now it was uncertain whether *Aeolidia* scents sea anemones or whether it may perhaps have directly been reached by parts of mucus or other fragments given off by the anemones. The cotton-wool experiments make it probable that the anemones are indeed scented, as fragments and mucus must have been sieved out by the cotton-wool. The greater difference between damaged and undamaged animals in series IIIb than in IIIa may be due to the fact, that the siphon end in the case of the damaged animals of series IIIb was *not* packed in cotton-wool, whereas the siphon end of the undamaged ones *was*, so that in reality damaged animals and an open siphon were compared with undamaged animals and a siphon closed by cotton-wool. Fragments or mucus of damaged anemones may therefore have been transported to the slugs through the open siphon, so that more scent was transported than by the water alone.

It is important that *Aeolidia* continues its way to the anemone within a siphon in which a concentration difference is wanting. This means that the scent of the anemone is chiefly used to stimulate the slug to migrate against the current and that this anti-current movement is continued though there is no longer a concentration difference. To take away all misunderstanding it should be added that the siphons were wide enough to give the animals the opportunity to return.

It should be added that the above facts tell nothing about the suitability of different anemone species as food for *Aeolidia papillosa*. Undamaged *Actinothoe* are apparently little attacked, though in my experiments damaged *Actinothoe* were regularly consumed.¹ I saw *Aeolidia* feeding on *Diadumene cincta*, but much less often and more slowly than on *Actinothoe*. I further got the impression that quite young *Aeolidia* did not flourish on *Diadumene cincta* and after my experiments were finished SWENNEN at Den Helder found that young *Aeolidia* did not use *Diadumene* as food, even when no other food was available for many weeks. VERWEY saw large *Aeolidia* attack *Tealia felina*, but according to his observations they prefer by far *Metridium senile*.

The method here used to demonstrate the preference of *Aeolidia* for one anemone or the other was finally used to see if the slug is also attracted by other individuals of its own species. The experiments sometimes gave the impression that this indeed may be the case.

¹ See also Postscript.

Special experiments gave no indication, however, that such an attraction by congeners plays a role. The slugs regularly crept into the control-aquaria in which no other *Aeolidia* were present, so that they occurred in quite variable numbers in all three aquaria. Accumulation of slugs must therefore apparently be ascribed (at least in most cases) to an increased emission of scent, due to damage done to the anemones.

IV. SUMMARY

The above experiments show that *Aeolidia papillosa* can find its chief prey, *Metridium senile*, from some distance, certainly by scent. It is more strongly attracted by *Metridium senile* than by the other species of anemones tested. It is not quite certain whether this is due to a difference in the character of the scent or to different strength of scent within the different species of anemones, though it is assumed that the character of the scent is of definite importance. Differences in strength of scent within one and the same species (*Metridium senile*) are certainly important, as wounded anemones attract more slugs than undamaged ones. It is of interest in this connection that young anemones attract more slugs than old ones.

A concentration difference in scent causes *Aeolidia* to migrate against a current. This anticurrent movement is continued when a concentration difference is wanting; this shows that the animals are not directed by the concentration difference, but by the current direction.

The experiments give no evidence that *Aeolidia* is attracted by the scent of congeners and so would find its food sooner than without their help. In such cases heightened scent-emission due to the attack of the anemones by the first-arrived *Aeolidia* will as a rule play a rôle.

Postscript: After this paper had been written miss Heikens found at Den Helder that cottonwool apparently may sieve a large part of the scent from the water. In this way the fact can be explained: that the figures for young and adult, and also for expanded and contracted anemones differ less in series IIIb than in IIIa and that the difference between wounded and unwounded *Metridium* is especially striking in series IIIb (in which cottonwool was used only in the case of the undamaged anemones).

Further, SWENNEN found indications that *Aeolidia papillosa* may show a different preference for *Sagartia troglodytes* and *Actinothoe anguicoma*. Since the possibility is perhaps not to be excluded (see footnote p. 163) that *Sagartia troglodytes* occurred among the *Actinothoe* used the results in respect to *Actinothoe* should be considered with caution.

ON THE ECOLOGY OF DISTRIBUTION OF COCKLE AND MUSSEL IN THE DUTCH WADDENSEA, THEIR RÔLE IN SEDIMENTATION AND THE SOURCE OF THEIR FOOD SUPPLY

WITH A SHORT REVIEW OF THE FEEDING BEHAVIOUR OF
BIVALVE MOLLUSKS

by

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I. INTRODUCTION

The extensive sand flats within the coastal areas of the southeastern North Sea, which are so well known under the dutch name of Wadden, are populated by large numbers of polychaetous worms and other species. Since the study of these areas is progressing in many directions the question arises what rôle animals play in their formation or change. This question is easier to put, however, than to answer. I will here try and deal with it in relation to two species of bivalve mollusks, which must be specially important in this connection because of their great numbers: the cockle (*Cardium edule* L.) and the mussel (*Mytilus edulis* L.).

As one cannot expect to gain an insight into the matter before understanding what rôle this special environment plays in the distribution of these mollusks, their distributional ecology will be dealt with first and the influence of the animals on their environment will follow thereafter.

In order to produce a base for useful conclusions the quantity and composition and also the source of the organic and other material suspended in the water, which is of so much importance to these problems, is dealt with in two separate chapters, whereas a special chapter is devoted to the feeding of these animals, which has been (and still is) the subject of many controversies.

I owe many thanks to H. POSTMA, chemist to the Zoological Station, and to Dr C. O. VAN REGTEREN ALTENA at Leiden, for some valuable suggestions made during the reading of the manuscript, and to Prof. Dr PH. H. KUENEN for revision of the English.

Some photographs, originally destined for this paper, were used for illustrating the Waddensymposium (1950) (cf. KUENEN, PH. H., in list of literature). They are referred to at appropriate places in the text.

II. ECOLOGY OF DISTRIBUTION OF COCKLE AND MUSSEL

I. THE ENVIRONMENT (compare map, fig. 6 p. 217)¹

If an attempt is made to characterize the Waddensea as an environment for marine animals in general matters may thus be stated:

1. Because of the shallowness of the area as a whole light can easily penetrate to the bottom. This opens the possibility for plant growth and the presence of plants means food and cover to animals. Animals can therefore be numerous. But these animals must be able to stand a

¹ Hydrographic data on the Waddensea are given by POSTMA and VERWEY (1950).

fair quantity of light and they must not be hindered by the plants as might easily be the case on the flats.

2. Generally speaking, currents in the Waddensea are rather strong (up to 4-5 km an hour in the western part) and oxygen and food are therefore easily transported to most parts of the area. But the animals must be able to stand these currents and this is especially difficult on a sandy bottom, which is constantly moving. The distribution of mussels, for instance, is greatly limited by that factor.

3. Currents are valuable, because they transport food. But this transport can only be important, where plenty of food is available. The food consists partly of plankton and partly of other material in suspension. This suspended material consists of organic debris, excrements of organisms, very fine sand, and clay. It forms one whole with the plankton which cannot well be separated from it, so that it is also difficult to distinguish between organic material contained within the plankton and that present as detritus. It is difficult to estimate the total volume of wet organic matter present in plankton and detritus as a percentage of the total volume of plankton and suspended matter, but it may amount to something like 70-90 %. Its importance is for a large part due to the organic detritus, the quantity of which in our coastal waters is very high. Why it is so high has never been definitely established. It is generally assumed, I think, that it is due to plants (especially *Zostera* and algae). In my opinion, however, the mixing of fresh and salt water has also something to do with the matter. Where these meet their plankton is partly killed by the change in salinity, temperature or some other factor. As the quantity of fresh water partaking in the mixing is small compared with that of the sea water the latter must be the chief producer of the organic matter. POSTMA (1951) has pointed out that within the Waddensea it is transported against the gradient and accumulated within the quiet inner parts. It is especially there that sinking takes place, so that the quantity present on the bottom is increased. Since there must be an equilibrium, however, between the large mass present on the bottom and the quantity present in the water in a suspended form, the latter quantity must also be high, notwithstanding the fact that currents there are weak. As the mixing of water goes on constantly the production of debris never stops. The question is dealt with in detail in chapter VI.

I suppose, then, that the mixing of water masses is the chief cause of the richness in food of the Waddensea and of coastal areas generally. The currents, combined with the shallowness of the area, keep much material in suspension, but in quiet places the latter is deposited. It is therefore available to those species which are able to use it suspended, as well as to those, which use it as a deposit. And since the quantity

of matter is so great the number of individuals can also be great.

4. The suspended matter, through its richness in organic material, is valuable as food to those animals which can use it, but at the same time it is detrimental to all organisms which are not able to stand its constant rain. Many species, especially among the hydroids, cannot work it away, except when helped by strong currents, and these are not found everywhere. The number of species is thus reduced because of the deleterious action of the so called silt.

5. The mixing of fresh and salt water during part of the year keeps the salinity relatively low and this is of advantage to those species needing such a condition, but it reduces the number of truly marine species.

6. The water of the Waddensea because of its shallowness largely follows the air temperature, and the temperature extremes certainly cause a further limitation of the number of species.

7. Because of the shallowness, again, part of the flats fall dry at low tide and these are exposed to quite extreme conditions: drying out, great variation in the quantity of light, excessive heat and cold, etc. Changes in water level, therefore, form one of the first factors limiting the number of species.

Summarizing, it may be stated that the Waddensea is inhabited by a small number of species, which can cope with (and possibly need) great differences in the quantity of light and suspended material, salinity and temperature, the strength of the currents and the changes in depth. But these animals have at their disposal extensive areas where competition with other species is less important than elsewhere and where food is abundant; they can therefore be numerous.¹ The distribution of both cockle and mussel should be seen in this light.

What rôle, now, do the factors involved play in relation to the presence and numbers of cockle and mussel?

2. THE NEEDS OF THE COCKLE

Cockles are limited to a sandy bottom, in which the animals dig themselves in. They lie hidden just below the surface, the siphons like short chimneys caring for the supply and removal of the water (fig. 4). The grain size of the sand, generally speaking, is not important (KREGER, 1940; SMIDT, 1951), but the bottom must lie in shallow water, a depth of about 3 metres forming the lower limit in the Waddensea proper,

¹ SMIDT, in a recent paper on animal production in the Danish Waddensea, which came out after my paper had been written, compares the Waddensea with some other coastal areas and he concludes that the Wadden are extremely rich.



Fig. 1. Cockle fishers at work naar Vlieland. Heaps of shells are lying everywhere around. July 1939, D. KREGER photo.



Fig. 2. Landing on the flats at sunrise, Sept. 1948. D. KREGER photo.



Fig. 3. Cockle fisher separating the shells from the cooked animals. D. KREGER photo.



Fig. 4. In- and exhalation siphon of a single cockle on the flats, tentacles expanded. The wide opening is that of the inhalation siphon. D. KREGER photo.

whereas they lived up to about 5 metres deep in the former Zuydersea; in the Scheldt estuary they apparently live deeper still and in the North Sea off Den Helder we found them up to about 14 metres deep. The reason for this depth limit is probably given by their need of light, but this has not yet been ascertained. Through this tie to shallow areas the animals on the Dutch side of the North Sea are limited to a narrow stretch of coastal water, including the inlets and the Waddensea.

Whereas their lower and outer limit is thus presumably caused by the absence of sufficient light their upper and inner limit may be caused either by the level of the sands or by salinity. Their upper level on the sands corresponds more or less to that of mean tide. They may occur in large numbers on flats falling dry for some hours every tide, but growth measurements clearly show that conditions are far from optimal where the upper limit is reached. They may also occur in the troughs on the beach of the Dutch west coast. — As to the salinity they stood less than 10 ‰ total salinity in the Zuydersea, but they remained very small there and conditions must have been adverse. When the Zuydersea was closed reproduction of *Cardium edule* still took place at a salinity of about 9–10 ‰, whereas all *Cardium* died when the salinity fell to between about 5.5 and 1.5 ‰ (compare HAVINGA, 1936, and SCHUURMANS STEKHOVEN, 1936).

Within the coastal area with its lower outer and its upper inner limit cockles occur in enormous numbers (figs. 1 and 3), but these vary strongly from place to place. This comes to the fore especially on the shallows of the Waddensea, where locally more than 1000 large cockles per square metre are found, in other places hardly any. One can probably state as a more or less general rule that few animals are found along the southern to western edges of the shallows; that a dense population may occur in stretches more or less parallel to the creeks at some distance from these (except along the southern and western edges); and that the remainder of the sands are thinly populated (see fig. 2).

Several different factors are probably responsible for this capricious „minor” distribution. The conclusions here given are based on the work of KREGER (1940), and non-published observations of miss BAGGERMAN, KREGER, KRISTENSEN and myself.

The pooriness of the population along the southern to western edges is certainly due to surf action. The bottom here is constantly in motion and there are indications that even larger animals cannot maintain themselves in such places.

The dense population at a certain distance from the creeks must probably be ascribed to the presence of favourable current velocities combined with a favourable depth. As to current influence, the young

cockles are accumulated in certain areas, where currents are weak. This does not necessarily mean that food conditions are favourable there, for when these cockles grow older, food may become insufficient at the place in question and stronger currents might be of more value; but it does mean that the settling of spat is largely influenced by the current velocity. – Also the depth over the sand is important, however, because current velocity and depth cannot easily be separated. Moreover, less shallow water means a longer period of submergence to the animals, which may result in better conditions for upgrowth and therefore smaller numbers of animals killed.

The thin, rather uniform population over vast stretches of wide flats, finally, must in the first place be due to the uniformity and strength of the currents moving over these areas, for the numbers of animals on such stretches may be higher in the current shadow of osier work than anywhere around. Possibly, the numbers here are also smaller than nearer the creeks, because so many young will have settled along the latter before reaching the wide stretches; this cause, however, I no longer consider of any importance, it could at its most play a rôle on vast stretches of sands like those near the island of Griend (fig. 6).

My former assumption (see KREGER, 1940, p. 188) that dense cocklefields may owe their existence to the presence of tide rips (for description and photographs compare POSTMA, 1950), in which the larvae (as well as the plankton generally) would become concentrated, so that they would settle at such places in enormous numbers, now has to undergo a change. It is now assumed that the weak currents within these tide rip areas permit the young cockles to settle there and they may at the same time be concentrated after their having been carried away from other places. My change of opinion in this respect is especially due to the work of miss BAGGERMAN, which will be published shortly.

The young cockles in the period of metamorphosis must have means to reach shallow water. THORSON (1946, p. 462–463) has drawn attention to the fact that larvae of marine invertebrates generally are positively phototactic when young, negatively when they grow older, in connection with their need after metamorphosis to seek the bottom. Those species inhabiting shallow water, however, would remain positively phototactic also as older larvae, and THORSON mentions as instances among others *Balanus balanoides* (certainly one of the very best examples), the polychaetous worm *Pygospio elegans*, the common mussel (the latter after SPÄRCK's observations), and some other species. These species, through their constant positive phototaxis, would be bound to the water surface and thus be able to reach shallow places. It would therefore be natural to suppose that cockle larvae show

a similar innate behaviour. In the summer of 1950 LUCAS at Den Helder has tried to find evidence for this assumption; his observations have not yet been fully worked out, however.

Also the burrowing behaviour of the cockle is interesting from the point of view of these young animals. During metamorphosis the shell measures some 250–300 μ . As the diameter of the sand grains varies from 10 to 400 μ or more, the tiny young creep over and between boulders comparable to those of cairns. These boulders, however large they may be in relation to the young cockles, are exposed to currents, strong enough to overturn and roll them. This may be the reason why the majority of the animals establishing themselves definitely are not 0.3, but some 1–2 mm, the younger ones apparently not getting hold except probably in very quiet places. These young of 1–2 mm, on digging themselves in with the help of their very long foot, disappear entirely below the uppermost sand grains, from where their siphons do not reach the surface. They apparently obtain their water through the grain interspaces.

It was stated above already that the young may easier settle where currents are weak than where they are strong, but that food conditions at places with weak currents are not so good, so that dense populations there may grow poorly or die. Even in places with stronger currents the density may greatly decrease later on for the simple reason that there is not sufficient place. ORTON (1937) and THAMDRUP (SMIDT, 1944, p. 19) found young cockles settling to the number of up to 100,000 per m², SMIDT (1951, p. 82 and 128) found up to 72,000, WOHLBERG about 70,000 and 40,000 per m². If 40,000 cockles of 1 mm shell length are placed close together they cover a space of no more than 20 × 20 cm. But one year later they need about 16 square metres, so that for the majority there is no place left. The maximum density shown by one year old cockles is about 2000 per square metre. The bottom, in which they live, seems paved then.

In conclusion, it may be stated that the cockle, because of its special needs, is much restricted in the choice of its grounds.

3. THE NEEDS OF THE MUSSEL

The behaviour of the mussel differs much from that of the cockle. Whereas the cockle digs itself in, the mussel as is well known attaches itself by means of chitin-like threads, which can be loosened again. These threads represent a remarkable semi-permanent form of attachment, which is also found in *Chlamys opercularis*, *Ostrea edulis* (KORRINGA and others), *Mya arenaria* (KELLOGG, 1901, SMIDT, 1951) and even *Cardium edule* (JOHNSTONE, 1899, SEGERSTRÅLE, 1928). But in all these

species thread-spinning is limited to early life (in *Chlamys* according to our own observations it may also occur in halfgrown animals), whereas in mussels it remains. Attachment is difficult or impossible on a sandy bottom, which is constantly moving. But where stones or other bivalves cover the ground these form a suitable substratum to the mussel, especially cockles being very important in this respect. Mussels, once settled, may at their turn form a firm base for later individuals.

Like the cockle the mussel is limited to shallow water, from somewhat below high water¹ to a depth of some 6–9 metres. As an exception large banks may occur in somewhat deeper water, of up to 17 metres or perhaps more (northern part of Texelstroom, see map). In the North Sea at some distance from the coast mussels are wanting, except near the surface on the hulls of buoys and lightships.² From analogy with the cockle I have always assumed that they do not occur at the bottom there because the latter (at 20–25 m depth) does not receive sufficient light, but proof is still wanting and it must be admitted that they are absent also at the bottom nearer the coast, except where piers, etc. occur. In this connection KRISTENSEN draws my attention to the fact that old mussels can apparently live in the dark, whereas cockles probably can not. The reason for the absence of mussels in deeper water might therefore be that the young do not settle in a dimly lighted environment, where as old animals they would be able to live. This seems unnatural from the viewpoint of the biological significance of such behaviour. – It has more than once been supposed that mussels hardly live outside the tidal zone, because the starfishes (*Asterias rubens*) destroy them there. Whereas this may hold good for certain localities the downward limit of 6–17 metres below low tide level in the Waddensea cannot be caused by starfishes, since the latter occur in great numbers also at 4 metres depth, where mussels may be numerous. Moreover, the cockle, which has a similar depth limit, is not preyed upon by starfishes. Anyhow, one can say that mussels, like cockles, are limited to a narrow coastal zone including the inlets and the Waddensea.

In the Zuydersea mussels diminished rapidly in numbers at the entrance to the southern part, where the salinity fell below 15–20‰. After closure *Mytilus* was killed from the moment the salinity fell to 9‰ and all animals were dead when the salinity had fallen to 6 (HAVINGA, 1936, p. 10). Judging from the distribution in other areas (Baltic, Danish waters) the extreme lower limit is about 5‰, but this

¹ FISCHER (1929, p. 113) states that in quiet water the upper limit lies somewhat below the low highwaters' of neap tide.

² SCHRADER (1911) mentions a young individual from a depth of 42 m in the North Sea some 30–40 miles from the coast (Oystergrounds). He supposes that it was carried to that place as a larva.

is far from optimal, and animals found in such salinities remain quite small. Apparently, there is much agreement between cockle and mussel in respect to their salinity needs, but judging from their distribution and behaviour in the Zuydersea the mussel cannot stand such low salinities as the cockle.

SEGERSTRÅLE (1942) mentions 4.5‰ as the lower limit for total salinity stood by *Mytilus edulis* on the finnish coast. The more brackish the water there the smaller the animals are. DODGSON (1928), FOX, MARKS and AUSTIN (1936), and FOX (1941) have shown that mussels can only cope with such low salinities if they have quite gradually grown accustomed to them.

FOX (1941) showed that the Californian mussel may grow accustomed to Cl'-concentrations of between about 9.4 and 28‰, i.e. about 17 and 50‰ total salinity (seawater has about 30-35‰ total salinity). Between these values the relation Cl' in tissue water: Cl' in seawater is about 1:1.6; below 17 and above 50‰ this relation is not maintained and FOX believes that the animals do not survive this condition for somewhat longer periods. It follows from these observations that *Mytilus californianus*, which does not occur in bays and estuaries, but inhabits the open coast, has a much higher salinity range than *Mytilus edulis*, which is limited to shallow coastal water. Physiological and ecological differences therefore go hand in hand.

Though *Mytilus californianus* in experiments stands salinities as low as 17‰ the species in nature hardly occurs below 30‰. FOX (1941) has assumed that it does not occur in water of lower salinities, because for the sexual products and development higher salinities would be needed. This assumption has been tested by YOUNG (1941), who observed that gametes and young larvae live longest in water of 33.5 and 29.6‰ and that already in water of 25.1‰ conditions are not so good; fertilization may as a rule still occur in 21.5‰, but the survival of the larvae at this concentration is distinctly lower. In one experiment, however, Young obtained fertilization of some few eggs in water of only 9.1‰ salinity. Though, therefore, it may be true that sexual products and young larvae need higher salinities than the lowest ones stood by the old animals, it is clear that the reason why the old animals in nature do not occur below about 30‰ must probably not be sought in the needs of the gametes or young larvae. YOUNG, after citing others, concludes that surf action, common on the open coasts where *Mytilus californianus* occurs, may be needed.

The mussel does not inhabit the whole of the coastal area (in so far it is sufficiently shallow) in equal numbers. In this respect it does not differ from the cockle. The minor distribution of both species, however, is totally different. If one determines the density of cockles over extensive flats it is striking how gradually it mostly changes along a traverse. Nothing like this holds for the mussel. It occurs in patches of large beds or small scalps, in which thousands or some very few animals may be accumulated. There is always local concentration, with areas or patches without mussels between. As to the distribution of these patches as a whole there seems at first sight to be no system in it at all. Observed through the eyes of a geomorphologist, however, two facts are obvious. They are well illustrated in photographs 11 and 12 of the Waddensymposium. The first is that the patches are often

bordering creeks, the second that many of them are lying across the drainage channels of large shallows. Here they may form incomplete dams of up to 200 metres long. The longitudinal axes of the separate musselbeds are lying parallel to the longitudinal axes of the dam. The dam may be several beds broad and the beds forming it are, I believe, distributed in the most haphazard way. The breadth of the dam may amount to some 50 metres. Whereas, in many cases, therefore, the situation of musselbanks in one way or the other bears some relation to that of creeks, there are also patches of banks which cover part of an extensive shallow, apparently without a creek as starting point (Wadensymposium, photograph 10).

Here also, it is logical to ask for the reason of this special distribution.

There is little doubt that it is a question of current velocity in the very first place. KUENEN (1942) has shown that mussels on a sandy bottom cannot maintain themselves where currents are strong and that food conditions are poor where currents are weak. Where mussel beds are situated along the slopes or edges of creeks the influence of currents is clear enough; where dams of mussel banks cross important drains I am inclined to assume that the dams grow up where current conditions are optimal. In the case where a creek is absent, finally, the part of the flats covered by mussels apparently always has currents differing from those over the rest of the flats. All this, however, should be confirmed by more observations, and, if possible, by experiments in the field.

Judging from what is found in the cockle and bivalves generally, one expects that also in mussels the decision where the animals will settle must fall within the first weeks after metamorphosis. The question may be raised, then, how a musselbed can be formed through the action of thousands of mussel larvae more or less uniformly distributed in the water. For there can be no doubt that the distribution of the larvae after a stay of some weeks in the plankton may be called uniform. My original assumption was that the mussel would have a social instinct based on something like smell, and that through it the animals congregate into dense banks. MAAS GEESTERANUS (1942) has shown, however, that this is by no means the case and that banks are formed from mussels, which are accidentally carried over the place in question and find a firm substratum for attachment there. His observations may thus be summarized.

Mussels, because of their method of attachment, prefer to settle in niches. While quite young they can do with small spaces and large numbers settle in the branching of hydroids and algae. I do not think that their preference for such frame work is based on the right niches only, but a certain preference for them is clear. However, they dis-

appear from this substratum after some time, apparently by loosening their hold. This tallies with the fact that large numbers of young mussels of from 0.5 mm and smaller, but up to 10 mm in length or more, are transported through the currents. MAAS GEESTERANUS found more than once 50-60 animals settling on one group of 4 roof tiles (placed on the flats) within one single highwater period. As it is more than improbable that mussels of 0.5-10 mm length would not have passed an earlier period of attached life there is little doubt that the animals found had loosened their hold at other places. Assuming this supposition to be correct it does not seem unlikely that such an alternation between fixation, detachment, transport, and new fixation, may repeat itself several times and new observations, made near Den Helder by miss COOL in the summer of 1950, favour this assumption. It is probable from them that the somewhat older young mussels prefer places, different from those inhabited by the smallest and also from those inhabited by the larger individuals. As to these larger animals, there is probably only one substratum which wholly satisfies their need for niches: the musselbed itself. The animals congregate on them through their need of a suitable place of attachment; it must be assumed that such beds are built up through the action of thousands of individuals, carried over them by chance. T. C. NELSON (1928) described for young *Mytilus* of up to nearly 1 mm in length the formation of a gas bubble by the gills, which would help the animals in floating; but here we are dealing with animals of up to 1 cm and more and it is not clear how such animals can be so easily transported.

In connection with the above facts it is of interest that the process of building mussel beds may show some difference between old, existing beds, and young new ones.

As to old beds, there are a number of places in the Waddensea where these probably exist for many years. Part of them may remain undamaged for several years, others may be broken down again and again during the winter season, but the firm base is not easily destroyed and a certain number of living mussels may remain. The reasons for such damage have been given by FIELD (1923), who mentions storm or strong currents in winter, shifting sand, floating ice, frost, and some other factors working also during the remainder of the year. Such old beds apparently become covered by very few mussels of smallest size; they probably grow chiefly through the arrival of somewhat larger mussels.

There are also localities, where old mussels are absent, but where conditions are quite suitable for the settling of young brood, for instance where a dense field of tubes of dead *Lanice conchilega* covers the bottom or where a cockle bank has entirely died through frost. Here

thousands of young mussels of one and the same size may grow out to extensive patches of some thickness (Waddensymposium, photographs 8-9). They may be well on the way to become true musselbeds when storms come, and most of these patches are rolled up by the action of wind and currents, and their mussels are carried away. The chief reason for their destruction certainly is that these beds are situated in much exposed positions; they can, therefore, grow up in quiet periods, but are destroyed again in stormy ones. So, we cannot say that young mussels do not form beds, but the beds they form are easily destroyed again and make place for new ones. The mussels, which formed them, will gradually contribute to the importance of old beds, which chiefly grow through the addition of somewhat larger animals.

The representation here given for the younger beds is especially based on observations of KREGER and myself, made in 1939 (compare also KREGER, 1940); that given for old beds is based on the vision of the fisheries surveyor for the western part of the Waddensea, who believes that a number of old beds do remain for years. Probably, however, there are many interstages between one group and the other. KREGER (1940, p. 182-184) described two extensive cockle beds of great density which he found in September 1937 at the Staart van Schieringhals. They consisted almost entirely of cockles born in 1936. Both were recognizable from far as a dark stretch, the dark colour being caused by algae (*Enteromorpha*, *Cladophora*, and others), which found a firm hold on the cockle pavement, chiefly on its dead cockles. In the centre of one of the beds a young musselbank had established itself. Returning there in the summer of 1939 KREGER found that both cocklebeds had been transformed into musselbanks, estimated to be 0.75-1 metre high. Many of the mussels had been killed by the frost of the past winter and here and there heaps of shells had been washed together. A small bank of partly dead cockles and clusters of mussels was found at about 200 m from the first in northeastern direction and it looked as if a southwestern storm had carried them there from the chief bank. In this instance, cocklebeds had grown up on these flats in 1936, a year in which there was an enormous brood fall of cockles everywhere in the Waddensea. These beds had grown to a hard pavement in 1937, when a field of young mussels began its development on the pavement of one of them. In 1938 the second bed also showed a musselfield and both these musselfields grew up to heavy banks in the course of that summer. Notwithstanding the fact that part of the mussels were killed by the frost and carried away the banks next summer had a height of 0.75-1 metre.

This course of events is no more than an instance of the second possibility mentioned above, with the only difference that the mussel-

banks maintained themselves for a longer period. In many places such a course may even be the general rule. FIELD says that musselbanks may disappear entirely 3-4 years after they grew up, to give place to new banks again. In the Waddensea it is not uncommon, I think, that there is a regular alternation between cockle and musselbanks in such cases. The cocklebed is covered by mussels when the cockles are lying dense enough to form a hard pavement. This pavement gives the mussels a firm hold, but when their bank grows higher and higher it is exposed to so many dangers (frost, drying out, shortage of food, increased exposure against currents) that it can no longer withstand them. The mussels are carried away, together with the dead *Cardium* shells, and the sands are lying bare to receive a new cockle population next spring. Because there is ample place a dense bed of *Cardium* can again develop and the whole course of events may repeat itself.

In conclusion, it is more than clear that the needs of the mussel, notwithstanding the fact that the species is so widely distributed, are no less special than those of the cockle and that the mussel, like the cockle, is therefore as restricted in the choice of its grounds.

III. THE QUANTITY AND COMPOSITION OF THE MATTER SUSPENDED IN THE WATER

The different distribution of cockle and mussel must result in a more or less different influence of both species on their surroundings and it may be asked whether this influence is reflected in the formation or growth of the area studied.

Before dealing with this question two series of facts must be considered in some detail. One is concerned with the quantity and composition of the material suspended in the water, which is of so much importance to the animals studied. The second deals with feeding problems, which should form the base for a correct understanding of what happens to the suspended material pumped in by them. The latter chapter has become more detailed than would be necessary in connection with the problems discussed. The biology of feeding in bivalves represents a field with so many points of interest and at the same time so many controversies, however, that a fuller review appeared justified. It follows in chapter IV.

As is well known lamellibranchs obtain their food from organic material in the water or laid down on the bottom. Such species as *Scrobicularia*, *Macoma*, *Angulus* (*Tellina*) and *Abra* by means of their long siphon suck in the material laid down on the bottom, whereas such species as mussels and cockles, like clams, oysters, and many others

TABLE I

Loss on ignition in percentage of total quantity of suspended material and plankton, dried at 120° C

Date	Depth	EBB Total quantity of matter in 1 l, dried at 120°, in mg	Loss on ignition in percentage of total	FLOOD Total quantity of matter in 1 l, dried at 120°, in mg	Loss on ignition in percentage of total
1938 June 2	0.5 m above bottom	59	20.2	138	22.9
3		212	13.5	371	16.4
7		205	11.4	186	15.8
8		277	14.2	562	13.4
9		88	15.9	457	26.4
June 21	mean 1 m below surface		15.—		19.—
22		23	18.6	37	16.5
23		18	19.—	50	16.—
24		50	17.3	62	19.—
27		47	18.2	47	18.7
		15	20.4	503 (sand!)	7.7
	mean		18.7		
Oct. 21	1 m above bottom	61.4 (mean for 14 samples, taken every half an hour of the ebb period)		61.3 (mean for 12 samples, taken every half an hour of the flood peri- od)	15.6 (without the figure of 7.7 the mean is 17.6%)
	1 m below surface	51.2 (mean for 14 samples, taken every half an hour of the ebb period)		44.4 (mean for 12 samples, taken every half an hour of the flood peri- od)	mean loss on ig- nition for ebb and flood taken to- gether 16.5
1940 June 5	1.5 m above bottom	mean 17.5 (be- ginning of ebb) mean 77.4 (strong ebb) mean 35.9 (ebb)	17.— 4.4 12.2	18.4 (beginning of flood) 52.5 (flood) 21.9 (end of (flood)	14.7 6.7 9.7
		mean 24.0 (end of ebb)	12.6		
	0.5 m below surface	mean 16.0 (be- ginning of ebb) 21.1 (whole of ebb)	5.6 11.4	18.0 (low values flood) 48.8 (high values flood) 15.6 (low values end of flood) 32.9 (high values of flood)	9.2 8.9 17.0 11.2

take their food directly from the water by pumping the latter in and retaining the food. Before proceeding to their influence on this food, we will deal with the food itself first.

It was already stated in chapter II that judging from microscopic examination the total volume of wet organic matter present in plankton and detritus may amount to something like 70–90 % of the total of plankton and suspended matter together; it is only a rough estimate and therefore without much value. As this organic material contains much water (perhaps some 95 %) it forms no more than a small percentage of the total of a sample dried at 120° , as will follow below.

The figures of table I relate to the water of the Nieuwe Diep, the harbour of Den Helder. The latter is no more than a creek of the Waddensea with dams on both sides. Strong ebb and flood currents run through it as is the case with other creeks, but the quantities of suspended matter may differ from those of other creeks, because land with sluices and fresh water are so near by. The figures for the harbour are the only exact figures available, however. They have been obtained by J. SCHEELE (as a chemist to the Rijks Waterstaat stationed at the Zoological Station) from samples collected in June and October, 1938. A series of samples from June, 1940, have also been analysed, but in a less detailed manner, so that only the total quantities of solid matter, not the composition, are given here. The depth at the place of sampling was about 6 metres.

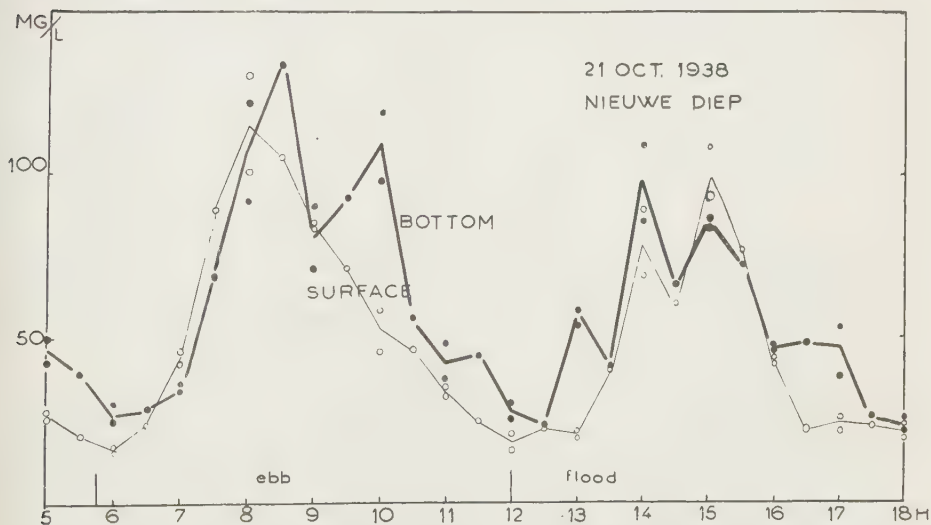


Fig. 5. Quantities of total suspended matter (plankton included) in the Nieuwe Diep, 21 October 1938, according to determinations of J. SCHEELE. The figures are expressed in mg dry weight per litre of water.

The curves for 21 October 1938 (compare fig. 5) show that there exists – as is well known – a direct relation between the total quantity of suspended matter (plankton included) and the current velocity. The figures for 21 October 1938 further show that the total quantity is about the same at one metre below the surface as at one metre above the bottom, in other words, the quantity is rather homogeneous down to about one metre above the bottom. The loss on ignition, in which the organic material is contained, forms some 10–20 % of the total. The loss on ignition tends to be low when the total quantity of matter is high, and inversely. This means that high total figures are in the first place due to an increase in the quantity of *inorganic* matter.

The composition of this inorganic material (determined from the same samples) may be deduced from the details of table II. Because the separate samples contained too little material to be analysed separately the quantities of matter of all subsurface samples and those of all bottom samples were mixed and analysed together so that no difference between the quantities present during ebb and flood can be given.

TABLE II

Composition of inorganic constituents of suspended material (plankton included).
The figures represent percentages of the ignition residue

Depth	SiO ₂	CaO	MgO	Al ₂ O ₃	Fe ₂ O ₃	Total
0.5 m above bottom (June 2, 3, 7, 8 and 9, 1938) .	62.98	10.21	0.42	6.80	19.66	100.07
1 m below surface (June 21, 22, 23, 24, 27, 1938) . .	42.69	6.83	1.41	6.53	38.48	95.94
1 m above bottom (October 21, 1938)	75.6	12.8	trace	2.82	7.65	98.87
1 m below surface (October 21, 1938)	68.8	21.8	0.2	4.21	2.93	97.76

Bij accepting for clay the formula $\text{Al}_2\text{O}_3 \cdot 2\text{SiO}_2 \cdot n\text{H}_2\text{O}$ one can calculate how much of the SiO₂ may be considered to belong to the clay, how much to the sand. The above table then reads as follows (table III).

The quantity of sand even in the surface water is quite variable, and, relatively speaking, nearly always important. The quantity of shell material (in any case that of lime) may be as variable as that of the sand. The percentage of clay (determined as $\text{Al}_2\text{O}_3 \cdot 2\text{SiO}_2 \cdot n\text{H}_2\text{O}$) is rather low through the high figures for sand; quite remarkable, finally, is the great quantity of Fe₂O₃ (probably present as iron hydroxide), which may amount to nearly 40 % of the residue remaining after ignition, or some 32 % of the dried total, the loss on ignition included. Up to

1950 I have always been of opinion that this high percentage of iron-hydroxide in the suspended matter of the Nieuwe Diep might be due to the fact that the creek is used as a harbour, with many ships and all kinds of steel work, and that the suspended matter in the Waddensea itself would contain much less of this material. This vision was supported by the fact that SCHEELE found similar high values (27.5–30 % of ignition residue) for the suspended matter in the water of the harbour of Zeebrugge (Belgium). Before this paper went to press, however, POSTMA – doubting the correctness of this assumption – determined the percentage of Fe_2O_3 in the suspended matter of water samples collected June 1949 at Texelstroom. He found values of 20–35 (average 25) % (expressed as percentage of the dry weight). – SCHEELE found much lower values for October than for June. Since this might indicate an important annual variation POSTMA also determined the percentage present in winter. As winter samples from the Waddensea were not available at that time he used samples collected in the Nieuwe Diep. These samples (taken February 9, 1950) gave the same high percentage of Fe_2O_3 for the suspended matter as the summer samples from Texelstroom: 26–33 % of the dry weight.

TABLE III

Composition of inorganic material. The figures represent percentages of the ignition residue

Depth	Sand	Shellsand (CaO + MgO)	Clay	Fe_2O_3	Total
0.5 m above bottom (June 2–9)	57.20	10.63	12.58	19.66	100.07
1 m below surface (June 21–27)	37.14	8.24	12.08	38.48	95.94
1 m above bottom (October 21, 1938) . . .	72.3	12.8	6.14	7.65	98.89
1 m below surface (October 21, 1938) . . .	63.8	22.—	9.17	2.93	97.90

The determinations of SCHEELE and POSTMA, combined, show that some 55 % of sand, 12 % of shellsand (CaO + MgO), 10 % of clay and 23 % of Fe_2O_3 may be considered a rough average for the composition of the ignition residue. Because of the wide variation in the percentages involved, and the small number of determinations carried out, this figure is rather arbitrary, but it has some value for further calculations. Besides, the average loss on ignition amounts to some 17 %, but this percentage does not refer to the residue after ignition, but to the material dried at 120° C.

Numerous observations made in the Western Waddensea by H. POSTMA during the years 1946-'51 have shown that the average total of suspended matter (plankton included) may be estimated at about 25 mg per litre (dry weight at 120° C) and that the average loss on ignition amounts to 5.- mg. The CO₂ from the shellsand is contained in the loss on ignition and according to POSTMA's observations its weight is about 2.- mg, so that about 3.- mg remain. These represent organic material, since the water from the ironhydroxide – as has also been shown by POSTMA – is driven out through drying at 120° C.

The result is that the average quantity of organic material (3 mg) represents about 12 % of the total quantity of plankton and suspended matter together (25 mg per litre).

Accepting these figures as an average for further calculations and using the percentage for sand, shellsand, clay and Fe₂O₃, which were given above, the water of the western Waddensea may contain on an average:

Organic material	3
Sand	11
Shellsand (CO ₂ included)	4.4
Clay	2
Fe ₂ O ₃	4.6
Total	25 mg per liter.

The figures refer to the weight after drying at 120° C.

If the different constituents are expressed as percentages of the dry total of all suspended matter (plankton included) we find the following figures:

Organic material	12%
Sand	44
Shellsand	17.6
Clay	8
Fe ₂ O ₃	18.4

It should constantly be kept in mind that these figures represent rough averages and that they may show variation from place to place and in different periods of the year. The average figure of 12 % for the organic material is based on a large number of data, however.¹

¹ LINKE (1940) remarks the following: "Die Strukturanalyse zahlreicher Schlickproben (bottom samples) hat ergeben, dass 35 bis 70 % Diatomeenschalen, 3 bis 12 % organogener Kalk und ebensoviel organische Substanz im Schlick enthalten sind; die minerogenen Anteile treten oft stark zurück. Eine ähnliche Zusammensetzung haben auch die Sinkstoffe im Wattenmeer, nur dass hier die organogenen Anteile einen etwas höheren Anteil an der Gesamtzusammensetzung haben." This would mean that, Diatom shells included, at least 40–94 % of the suspended material in the Waddensea is organic. This seems a very high percentage and one would like to know what the word "Strukturanalyse" means and in how far these figures are comparable with ours.

IV. THE FEEDING BIOLOGY OF BIVALVE MOLLUSKS

We now come to the difficult question what exactly happens to this material through the activity of the animals. One cannot gain an insight into their actual rôle in matters of sedimentation without some fundamental knowledge of their feeding behaviour and the latter has been the subject of much controversy.

A number of points, which have already been enumerated in the general contents of this paper, are of interest in connection with this chapter.

They are dealt with below.

Research has chiefly concentrated on two groups of species: mussels and oysters. Very little work has been done on the cockle. As the principle involved is more important, however, than the actual facts, data on the oyster will be used wherever they may be of value.

I. HOW MANY HOURS A DAY DO THE ANIMALS PUMP?

This number has never been accurately determined, but a great many observations have been made on the times the shells are kept open or closed. Strictly speaking, open or closed shells are not representative for actual pumping, because pumping may go on while the shells are nearly closed and as an exception may stop when the shells are open.¹ On the whole, however, pumping goes on as long as the shells are open. This even holds for mussels at very low temperatures.

LOOSANOFF and NOMEJKO (1946) registered opening and closing of the shell in a number of specimens of *Ostrea virginica* in the field. They found that the animals kept their shells on an average open for more than 22.5 hours a day. NELSON (1921 and '23) and GALTISOFF (1926) found an average of 20, GALTISOFF (1928) of about 17 hours, due to the fact that in a few instances oysters failed to open during the 24-hour period. GALTISOFF's animals were kept in aquaria, however, those of LOOSANOFF and NOMEJKO and those of NELSON in the field. It should be added that the water temperature in all these experiments was rather high.

HOPKINS (1931) found for *Ostrea lurida* that the animals on an average kept their shells open for over 20 hours, LOOSANOFF (1939) found for *Venus mercenaria* a period of about 21.5 hours, LOOSANOFF

¹ For literature see DODGSON 1928, GALTISOFF 1928, HOPKINS 1933, and LOOSANOFF and ENGLE 1947. Whereas there is agreement about the fact that pumping may be stopped while the shells are open the data on pumping with nearly closed shells are controversial. HOPKINS stresses the point, however, that in *Ostrea gigas* no pumping takes place unless the shells are a little distance apart. "This distance represents the thickness of the mantle at the edge of the shell."

(1942) for American *Mytilus edulis* periods varying between 18.5 and 24 hours per day.

All these determinations show that, if possible, bivalves keep their shells open for more than 80 % of the 24 hours.¹

Shell movements are little or not influenced by the annual change of temperature, except that the shells may be closed at low temperatures and according to HOPKINS' observations (1933) also at high ones. HOPKINS (1933) observed that *Ostrea gigas* is open most of all at about 20° C and that it often closes below 6 and above 24° C, a point to which I return further on. Closing at low temperature was also observed by him (1931) in *Ostrea lurida*.

In this species HOPKINS (1931, p. 8-10) has shown that between about 7 and 17° C the temperature *as such* is of no influence on shell closing, though the influence of temperature *changes* is striking. The influence of one and the same temperature change (in this case of 2° C) is the greater the more the water temperature, in which the change takes place, approaches 7° C. HOPKINS gives no data for still colder water.

I think, his observations, combined with those of others, show that the temperature *as such* causes increased closing below 7-8°, whereas temperature changes of 2° are still active (though to a slight extent) in water of up to 17°.

That the shells may be closed at low temperatures has also been proved clearly by LOOSANOFF (1939) for *Venus mercenaria*, a species which closes constantly below about 3° C and is more or less constantly open above about 8° C. There is a clear relation between closing and temperature between 3 and 8°, and no relation between 11 and 28° C. - Closing at low temperatures was further shown by GALTISOFF (1928) to take place in *Ostrea virginica* (compare also page 196), whereas DODGSON (1928, p. 208) for *Ostrea edulis* described cessation of functioning below about 3° C. In the latter case extrusion of faeces and pseudofaeces was used as a criterion.²

According to the observations of DODGSON (1928) and LOOSANOFF

¹ HOPKINS (1931) found that one *Ostrea virginica*, tested for nearly two months (October-November) in running water, opened only 14.5 hours a day; two others, tested for 78 hours in summer, were open an average of only 10.4 hours a day; four others, in artificially aerated water, remained open an average of only 6.6 hours daily. He assumes that various factors may have been responsible for these low figures.

² NELSON (1923) states that a sudden drop in temperature may result in temporary decrease in the daily number of hours of activity. Between 4 and 6° C there is a sharp decrease in the ciliary activity of oysters, normal feeding occurs above this range, while almost no food is taken when the temperature of the water is below 4° C. Though these remarks give the impression that the *ciliary activity* was watched I suppose that conclusions were based on shell movements, since NELSON worked with an apparatus recording the shell movements of oysters in the sea. I did not see NELSON's publication of 1921, which probably gives further details.

(1942) *Mytilus edulis* behaves quite differently. DODGSON (p. 194) states that it has been observed to function normally at all temperatures between 0 and 26° C.¹ "At no particular temperature, or range of temperature, between the above limits, have they been noted to function especially actively or especially passively." DODGSON's further data (p. 194-207) go on to show that mussels may continue feeding and ejecting faeces and pseudofaeces in water temperatures sinking below zero. It will appear below, however, that mussels in water of about zero according to DODGSON may close during the day and open during the night only, and that in such cases active pumping takes place only at night.

LOOSANOFF found that American *Mytilus edulis* did not close their shell more than 25 % of the total time even at 1° C, that at temperatures between 0 and 1° a current of water was produced, that the cilia propelled small solid particles and that the stomachs of mussels removed from such cold water contained food.

It is clear from these observations that *Mytilus edulis* can cope with much lower temperatures than *Venus mercenaria* and *Ostrea virginica* and *lurida*. *Mytilus edulis* is a shallow water species with a northerly distribution and in connection therewith it must be able to stand great temperature differences and especially very low temperatures.

It was stated above that *Mytilus edulis* at low temperatures may close during the day and open at night only. DODGSON stresses the fact, emerging from a long series of observations, that mussels can be relied upon to open and function in the dark or in very subdued daylight, but not always to open during the day, especially when the temperature is low (p. 178, 187, 193-194, 201-202). They are as a rule open during the day when the temperature is 4°, frequently function in daylight at 1-2° C, and are usually closed in daylight if the temperature is at or below zero; in the dark, however, they are active in all these cases.

Such a difference between day and night was not found by LOOSANOFF (1942) in American *Mytilus edulis*, but LOOSANOFF (1939) found a similar behaviour in *Venus mercenaria*. The latter also closes its shell somewhat more during the day than during the night, especially between 5 and 15° C. It may perhaps be assumed that light and low temperatures cause closing, that high temperatures cause opening of shells and that at high temperatures the influence of temperature exceeds by far that of light.

The above observations show that oysters fully close at low temperatures, whereas mussels may close at low temperatures during the day only. In both cases there is increased closing at low temperatures. In

¹ Even at 26° C mussels were on one occasion seen to be actively feeding and passing faeces and pseudofaeces at a rapid rate.

this connection it is of interest that *Ostrea lurida* according to HOPKINS (1931) closes more during the daily hours of low than during the hours of higher temperatures, the average daily curves for water temperature and shell closing showing complete parallelism.¹ It is therefore clear that, especially in the oyster, decrease of temperature under all conditions gives increased closing.

When the temperature is not extraordinarily low shell movements are apparently little or not influenced by the rhythmic change of light during day and night. This is shown by observations of GALTISOFF (1928) for *Ostrea virginica*², of WEBB (1930) for *Ostrea edulis* and of LOOSANOFF (1942) for *Mytilus edulis* in America. LOOSANOFF cites WENRICH (1916) and CHIPMAN (1931) to the effect that also freshwater mussels show no different behaviour during night or day and LOOSANOFF concludes (1942, p. 233): "It indicates nature's provision enabling the mussels to keep their shells open at any hour of the daily cycle. If, because of the light, the mussels were compelled to keep their shells closed during the day, their feeding time would be confined to the hours of darkness only."

Especially sudden changes of temperature and also sudden changes of light may have a definite influence on closing (DODGSON, 1928: mussel; GALTISOFF 1928 and HOPKINS 1931: *Ostrea virginica* and *lurida* resp.). That LOOSANOFF (1939 and 1942) found no such effect in *Venus mercenaria* and American *Mytilus edulis* is not in contradiction to these findings, because the animals are apt to behave capriciously and hard and fast rules in this respect cannot be given. DODGSON, moreover, states that mussels show little or no response to artificial, only to natural light.

There is also an influence of mechanical and chemical factors, changes in PH or gas content, etc. (GALTISOFF, 1928). Especially the observations of GALTISOFF c.s. (1947) on the influence of pulp mill waste on the times of shell closing in *Ostrea virginica* are interesting, as are also those of LOOSANOFF and ENGLE on the rhythm of contraction of *Ostrea lurida* in high concentrations of micro-organisms with presumably toxic products. How DODGSON's observations (p. 191) on the influence of the changing tide on mussel activity must be interpreted I dare not say.

In such species as cockles and mussels, which may fall dry for con-

¹ HOPKINS supposes that also light may have had some influence on this phenomenon and his observations for *Ostrea virginica* seem to point in the same direction. His observations make probable, however, that temperature in this respect is far more important than light.

² NELSON (1921) was of the opinion that oysters (*Ostrea virginica*) are open less at night than during the day. Possibly, temperature influenced his results, but I did not see his publication.

siderable lengths of time, the number of hours of daily activity may be lower than those for bivalves which live constantly under water and for that reason a very low average, of no more than 12 hours of pumping per day, will be used as a base for the calculations following below.

2. WHAT QUANTITIES OF WATER DO BIVALVES PUMP PER HOUR?

The most complete details on this point are those of LOOSANOFF and NOMEJKO (1946), LOOSANOFF and ENGLE (1947) and GALTISOFF, CHIPMAN, ENGLE and CALDERWOOD (1947) for the oysters *Ostrea virginica* and *lurida*. They actually measure the quantities of water pumped. LOOSANOFF and NOMEJKO for *Ostrea virginica* found an average of 12.5-18, GALTISOFF c.s. (1947) an average of about 6-12 litres per hour. Nothing is remarked about the fact that these values are so much higher than those found after the same method by GALTISOFF (1928), with a maximum of only 3.9 litres per hour. The higher figures may be more correct than the lower ones, however, and the studies of 1946 and 1947 are of admirable thoroughness. Whereas the values mentioned above represent average ones, the maxima may be still much higher. LOOSANOFF and ENGLE mention one animal (*Ostrea lurida*) with a maximum of nearly 26 litres per hour for a short period, while 4 others pumped from 21 to 22.5 litres for a similar period of time. LOOSANOFF and NOMEJKO mention some animals (*Ostrea virginica*) pumping 25-27 litres per hour on an average, with a maximum of 31-34 litres per hour. The temperatures in the latter experiments were 19.1-25.8° C. LOOSANOFF and ENGLE stress the fact that very high values may be attained when clear water is available again after the animals have been in highly concentrated suspensions of micro-organisms for some time. This water apparently has the function of cleansing the animals (see especially p. 49 of their paper).

For the Californian sea mussel the quantity has been determined by FOX, SVERDRUP and CUNNINGHAM (1937). They used, contrary to GALTISOFF c.s., and LOOSANOFF c.s., an indirect method and their figures must be considered minima: they may be too low, but can not be too high. They find that at temperatures of 20-23° C mussels of 60-82 (average 74) mm pump 0.5-2.1 (average 1.4) litres per hour, that mussels of 95-130 (average 102) mm pump 2.2-2.9 (average 2.6) litres, whereas the 4 largest animals of 174-182 (average 178) mm pumped 1.8-18.1 (average 6.4) litres. *Mytilus californianus* becomes much larger than *Mytilus edulis*, which grows to about 90 mm only. Animals of 60-82 (average 74) mm may well be compared with about fullgrown Dutch mussels, and according to these investigations such animals would pump about 1.4 litres per hour.

JÖRGENSEN (1949), using the same indirect method, but somewhat simplified, finds some 0.16 litres per hour for *Mytilus edulis* of about 15 mm and some 0.75 litres for *Mytilus* of about 30 mm length. Temperatures for these experiments are not given. WILLEMSSEN (1952) used this simplified indirect method at Den Helder. He gave me permission to mention that mussels of 67–80 mm on an average pumped 1.8 litres per hour at a temperature of 12–15° C, whereas the maximum for an individual of 81 mm (at least for a short period) was 4.6 litres per hour.

A summary of some of these values is given here:

Length of animals	Number of litres pumped per hour
15 mm	0.16 (JÖRGENSEN)
32	0.75 „
48	1.1 (WILLEMSSEN)
67–68	1.7 „
77–80	1.9 „

JÖRGENSEN, in an earlier investigation (1943), found a value of about 0.04 litres per hour at 11–22° for small *Mytilus edulis* of about 0.2 g. In his table V he compares the quantity of water they pump with that of mussels of other sizes, neglecting the fact, however, that the youngest animals are no mussel but oyster larvae, and that the other observations relate partly to *Mytilus edulis*, partly to *Mytilus californianus*. These figures, therefore, should not be compared, but comparison of those for *Mytilus californianus* (taken from FOX, SVERDRUP and CUNNINGHAM) shows the same principle as that stressed by JÖRGENSEN: younger animals per gram of weight pump relatively much faster than older ones. Dr P. H. L. TAMMES drew my attention to the fact, however, that in these animals there is a linear correlation between the quantities pumped and the relative value for their inner surface, for which he takes the square of the cube root of their weight.

WILLEMSSEN also determined the quantity of water pumped by the cockle and he found an average of about 0.5 litres for old individuals of 30–40 mm length at 17.3–19.5° C. The maximum found was 2.5 litres.

It is of importance that the quantities of water pumped by one and the same animal may show much variation. MAC GINITIE ascribes this to the contraction of the gills. Complete contraction according to him shuts off the current of water entirely. But the quantities of water pumped also depend on other regulating mechanisms, which have well been summarized by LOOSANOFF and ENGLE: The rate at which the water passes through the oyster is controlled by the beat frequency of the lateral cilia of the gills, by the expansion and contraction of the gill ostia, the position of the edges of the mantle, and by the activity of the adductor muscle (which closes the shell). This is an admirable summary, to which one should add the expansion and flattening together of the gills in *Ostrea* (described for *Ostrea gigas* by HOPKINS, 1933,

see small print below) and the functioning of the velum in the inhalant and that of the septa in the exhalant opening in *Mytilus*, described below (small print this page, and p. 204). One should finally realize that all these forms of control are probably influenced by different factors, of which temperature and chemical (possibly also mechanical) influences may be the most important.

A good impression of the delicacy of the regulating mechanisms can be obtained from the detailed descriptions of DODGSON for the mussel. Three such instances are cited here.

DODGSON (p. 169) describes how at the base of the exhalant siphon two thin membranous septa occur, which may open and close the entrance to the siphon from within. "If the septa be watched (by artificial light) in a feeding mussel, they will often be seen to be performing more or less rhythmic movements of extension and retraction. The projection of fine suspended particles against the fimbriated margin of the inhalant opening may be followed by sharp extension of both septa, with almost complete momentary occlusion of the basal-slit." DODGSON (p. 170) could also observe that the movements of the inhalant velum (compare p. 204 of this paper) may be influenced by opening or closure of the exhalant septa.

On p. 170-172 DODGSON describes observations on the movements of the gills, which make it probable that the continuity of the walls of the suprabranchial chamber may be interrupted, so that the subpallial chamber is no longer subdivided. In such a case the inhalant and exhalant orifices become almost coterminous. The whole mechanism reminds one strongly of what may happen in the wall between the lower and upper branchial chambers of crabs (VERWEY, 1930, p. 226-228).

Again, on p. 166, DODGSON states: "There may be a definite reflex arc between the rectum or anus and the adductor muscle, as closed mussels, lying in water, have been noted to open a few millimetres, pass a faecal ribbon in the exhalant stream, and then quickly close again, and remain closed. In mussels taken out of water, after a "full meal", that is, with a full alimentary canal; and stored for some time, the rectum has been found to be engorged, apparently almost to bursting point, but no extruded faeces have ever been found in the mantle cavity."

Also HOPKINS (1933, p. 487-488) gives some detailed observations relating to *Ostrea gigas*: "When the most rapid current is being produced the gills are fully expanded and separate from one another. Then two of the demibranchs may be observed to flatten together, either partially or completely, and there is an immediate reduction in rate. Very frequently it was observed that the two medial demibranchs would flatten together and the two others press themselves against the right and left mantles, respectively. Sometimes this reaction would be momentary; at other times it could last for hours to a greater or less degree."

"Accompanying a sudden shell movement, the gills often contract far back as if to close completely the gill chambers. Such a contraction either alone or in conjunction with shell closure causes complete cessation of flow. GALTISOFF (1928a) noted marked changes in the rate of pumping which were probably due largely to movements of the gills. It may be also, as suggested by GALTISOFF, that mucus forms a layer over the gills, clogging the pores and impeding or stopping the current. Actually to observe this, however, is difficult."

There is a striking shortage in such detailed observations in the literature dealing with this subject and in invertebrate literature generally.

The quantities of water pumped may depend on quite a number of different factors.

Temperature influence on the rate of pumping in oysters has especially been studied by GALTISOFF (1928) and HOPKINS (1933 and 1935). GALTISOFF paid much attention to the influence of temperature on ciliary movement (compare in this connection also the footnote on p. 190 of this paper). Ciliary movement in *Ostrea virginica* may continue to below zero, but it becomes very slow and irregular then, and in the majority of oysters the current according to GALTISOFF stops when the temperature sinks below 8° , this being due to the lack of coordination of the ciliary motion. Generally speaking, the quantities pumped are highest at high temperatures ($25\text{--}30^{\circ}\text{C}$), and they are lower at 10° than at 20°C . The importance of this fact is well demonstrated by such work as that of SAVAGE (1925), showing that the quantities of food obtained by *Ostrea edulis* on the Suffolk coast are negligible during the period January–April, whereas appreciable quantities are taken from July to October, with a short period of brisk feeding in August and September. The temperature during these observations ranged from zero to 23°C .

HOPKINS observations on *Ostrea gigas* are of special value, because they give an analysis of temperature influence on both shell closing and ciliary movement. He finds that the quantity of water pumped depends on ciliary movement and the degree of openness of the shell and mantle. At a certain temperature there is a direct relation between the degree of openness of the shell and the quantity of water pumped. Temperature changes, however, have a different effect on shell opening and ciliary movement. Ciliary motion increases up to $27\text{--}28^{\circ}$ (as also found in *Ostrea virginica* by GALTISOFF), but the shells open widest at about 20° and a change of temperature from 20° to 25° causes a tendency for the shells to close, but produces at the same time more rapid action of the gill cilia, with the result that the effect on pumping is antagonistic. Below 20° an increase in temperature has more effect on pumping than one would expect from the increase in ciliary activity, but above 20° the effect on pumping is less. HOPKINS adds that both high and low temperatures (above 20° and below about 6°) appear to stimulate the oyster through sensory channels. It is quite difficult to keep a specimen open for experimentation either below 5° or above 25° ; the further from the optimum, the more difficult it becomes.

Also the mantle margin shows movements which influence the current. HOPKINS supposes that its tentacles have a function as receptors for stimulation by temperature, just as they possess receptors for stimulation by chemicals (HOPKINS, 1932 *a* and *b*). Mantle, adductor muscle and ciliary movement appear to be directly affected by temperature, but they all seem to act with a high degree of independence of one another, “with the result that variations in the rate

of flow are tremendous." HOPKINS finally refers to GRAY (1928), who noted that the amplitude of beat of *Mytilus* cilia decreases above 33° while the rate of beat continues to increase up to about 37.5° C. "This suggests a comparable difference in temperature optima concerned in the activity of single cilia, and emphasizes the complexity of the activities resulting in a single curve of gross activity at different temperatures."

LOOSANOFF's and DODGSON's observations on the state of affairs in the mussel were mentioned already. In this species the current goes on even below zero, but this need not mean that the quantities pumped cannot be smaller at low than at high temperatures. Observations in the aquarium at Den Helder, where living mussels are used for filtering the aquarium water, have given me the impression that they work little efficient at temperatures approaching zero.¹ Further, also the observations of VON HARANGHY (1942) are important from this point of view. He compares the capacity of *Ostrea edulis*, *Mytilus edulis*, *Spisula solida*, and *Cultellus pellucidus* to clear suspensions of a certain concentration at different temperatures. The activity of the oyster is lower at 10° than at 20° C, that of the mussel apparently somewhat lower, whereas *Spisula* and *Cultellus* at 10 and 20° C according to his results show no difference.

Chemical influences on the quantities of water pumped are also important. It follows from VON HARANGHY's observations that mussels and oysters are less active in clearing suspensions from their suspended matter when the salinity of the water is low than when it is high. The results of GALTISOFF c.s. prove that solved products of pulp mill waste in higher concentrations decrease the quantities pumped and that the latter directly depend on the waste concentration. This effect, too, is certainly due to a direct action on the cilia. — LOOSANOFF and ENGLE show that also the concentration of the suspension within the water in which the animals live is of much influence and that very high concentrations may even bring pumping to a standstill. They assume that high concentrations work chemically and mechanically. That they may work chemically has been proved by the fact that the filtrate of their cultures had the same effect as the cultures themselves or the cells only.

¹ It follows from determinations made at Den Helder in 1951 by miss HEIKENS that the quantities of water *Mytilus edulis* pumps at or near 0° C are indeed small and of no importance when compared with the quantities pumped at 10 – 15° . The data will be published in Archives Néerl. de Zoologie.

DODGSON (p. 178) states that under similar temperature conditions mussels clear tank water more quickly in September–October than in February–March. He seeks the explanation in gonadal development or some other influence. Such an explanation does not hold for the observations at Den Helder, where temperature clearly is the operative factor.

This chemical influence is wholly comparable to that of pulp mill waste. That they also work mechanically has, I think, not been proved with certainty, a conclusion apparently also reached by KORRINGA (1949, p. 240). This does not mean that mechanical influences cannot be of importance, of course. It is probable that they do play a rôle.

3. WHAT PART OF THE SUSPENDED MATERIAL PRESENT IN THE WATER IS PUMPED IN?

Is the water pumped in with all the material suspended in it or does selection take place at the margin of the siphon?

So many observations have been made on so many species now that there can no longer be any doubt that selection at the siphon entrance is of hardly any importance. It is certain that the animals do take in all particles below a certain size without any selection, if they are not chemically or otherwise dangerous. Very little attention has been given to the point what is actually refused, however. COE and FOX (1944, also COE 1945) state that relatively large and spiny objects are prevented from entering the inhalent opening, but what size is refused by what animals is unknown. According to COE (1947) the inhalent siphon of the Pismo clam (*Tivela stultorum*) is provided with an elaborate filtering mechanism, with sensitive branching papillae which prevent the entrance of larger particles into the mantle cavity. Similar tentacles are found in *Cardium*, *Mytilus*, *Ostrea*, and certainly in other species, but it would be worth while to give this mechanism more attention, especially as it also contains the sensory mechanism which gives the stimulus for contraction of the mantle and adductor muscle of the shell, as was remarked by ALLEN (1921) and HOPKINS (1932, 1933). HOPKINS studied it in *Ostrea virginica* as to chemical stimulation.

It is well known that in plankton investigations it is not so easy to obtain a good idea of the true composition of the plankton present in the water, because fine meshed gauze throws part of the water out, coarse nets do not catch the small animals, whereas the narrow opening of the hose attached to a plankton pump may give such animals as Copepods the opportunity to escape. In this connection the following remarks of SAVAGE (p. 15) are important. "It will be observed that during the summer months when the temperature was high, and the feeding activities of the oysters were at their maximum, quite considerable quantities of metazoa (by volume) were captured. After October they disappeared from the food contents, and this was doubtless due, as MÖBIUS (1877) and NELSON (1920) have suggested, to the weakening of ciliary and muscular action caused by the fall in temperature, with the result that the oysters had no longer the power to capture the larger

organisms." This possibility, that the Copepods, etc. in August-September could no longer escape because the oysters pumped so very fast, should certainly not be neglected. A second possibility, however, may be that the larger animals were caught in greater numbers, because so many litres were filtered; also the diatoms and detritus show high maxima in the same months. I have not tried to analyse SAVAGE's figures in respect to the two possibilities mentioned. It is clear from his data that the large summer-numbers of Copepods, etc. were not due to the greater numerousness of these animals in the water during these months.

Speaking generally, it is quite probable that nearly all the material reaching cockles and mussels as suspended matter is pumped in. This is important in connection with the calculations, which follow below.

4. WHAT PART OF THE MATERIAL PUMPED IN IS RETAINED?

Next comes the important point what part of the food is retained from the water before the latter leaves the animal again. This point is full of controversies.

MAC GINITIE has defended the view that pumping need not mean feeding, as a lamellibranch may be pumping without retaining back the food suspended in the water pumped, because the layer of mucus over the gills, which according to MAC GINITIE is necessary to feeding, is not always present as a continuous sheet. COE and FOX (1942) also state that experiments at Scripps Institution, California, showed that the mussel *Mytilus californianus* does not feed all the time it is actively pumping water through the gills.

There are indeed a number of observations, showing that all the matter pumped in need not be retained (GALTISOFF, 1928; LOOSANOFF and ENGLE, 1947), though in other cases it is, and this is one of KORRINGA's arguments (1949) for believing that MAC GINITIE's view is right. "We should say with MAC GINITIE: certainly it never should be said that a pelecypod is feeding just because it is pumping or maintaining a current through the mantle cavity." It must be said that GALTISOFF's observations (1928), according to which larger particles like small diatoms seemed to be retained, anyhow, whereas small particles gave quite variable results, could be explained by the assumption that small particles can pass the gills more or less unhindered when the mucus layer is incomplete, whereas larger ones could then be retained through the fronto-lateral cilia. This is what MAC GINITIE, KORRINGA, and also JÖRGENSEN actually suppose. JÖRGENSEN has tried to prove the correctness of this assumption. His results, however, are not convincing, since he does not reckon with the possibility that the mussel itself

interferes by either retaining material or letting it through in another way than through secreting mucus. Moreover, his experiments with flagellates are partly in contradiction to his conclusions.

The whole question of retaining food may remain doubtful as long as no better experiments have been made. MAC GINITIE himself is of opinion that the ingestion of such substances as carmine and carborundum never takes place in normal feeding. But so many non-nutritive kinds of material, carmine included, have been found to be readily ingested, that we must at least try to bring the numerous former observations into line with the new ones and not discard them without more.¹

It is certain that all kinds of material, at least down to the size of large colloids, can be retained. ZOBELL and FELTHAM (1938) have shown that *Mytilus californianus* can live for long periods on nothing but bacteria and on this food can gain somewhat in weight. They even kept mussels alive for two years on a diet of bacteria. DAMAS (1934) concludes on good grounds that cockles strain the colloids from the water. We are probably allowed to say that the same happened in the experiments of FOX, SVERDRUP and CUNNINGHAM, and those of JØRGENSEN. FOX and COE (1943, p. 236), finally, proved in "preliminary experiments" the mussel's ability to remove from its medium very fine, uncentrifugable colloid material such as Congo Red or boiled "soluble starch" in highly diluted dispersions, ingesting some of this material and expelling the rest as pseudofaeces. They even believe that colloids may be a quite valuable source of nutrition. Its value must remain uncertain, however, as long as the quantity of such matter present in the sea is not known.

Not only can lamellibranchs retain material down to the size of colloids, they can strain this off so efficiently that the material can apparently be eliminated completely during one single passage of water through the gills. FOX, SVERDRUP and CUNNINGHAM conclude that in their experiments a constant amount of water passed through the mussel chamber in unit time and that virtually all suspended (and colloidal) calcium in this amount of water was removed.

On the other hand, the observations of LOOSANOFF and ENGLE show that in dense concentrations of micro-organisms high percentages of the suspended organisms may pass through the gills without being retained.

These controversial results could be explained through the supposition that the animal can change the quantity of material it retains

¹ Thus mussels have been observed to gorge their alimentary canals, so to speak, with chalk; not only for hours, but for days on end (DODGSON, 1928, p. 165); compare also DODGSON, p. 182-185.

more or less "at will". This could be effected through the secretion of mucus, as supposed by MAC GINITIE, or perhaps in another way: through the action of the fronto-lateral cilia, by opening the wall between both branchial chambers, etc. It would mean that, as a reaction to the presence of unsuitable material not only the shell or mantle could be closed, or the siphon shut off, but also mucus production could be stopped, the action of the cilia changed, etc. It follows from the experiments of GALTISOFF *c.s.*, and of LOOSANOFF and ENGLE, that the stimulus which leads to shell closure can be quite different from that which causes ciliary standstill. Highly concentrated suspensions might cause ceasing of ciliar straining or of mucus secretion, though pumping might go on. In such cases large quantities of suspended material might pass the animal partly unhindered, though a certain percentage of them would be retained. The latter might be partly rejected, but another part might find its way to the intestinal tract. In such cases large quantities of the suspended matter could be found in the outgoing current, as well as in both faeces and pseudo-faeces. This is what actually happens. If the water would contain suitable and unsuitable material at the same time, now one, then the other stimulus would predominate and matters would become still more complicated. Mucus secretion, the action of the fronto-lateral cilia, contraction of the gills, opening the chamber walls, would all form means to deal with suitable as well as unsuitable food through the control of the innate reaction mechanism of the species. Feeding would not be restricted to periods when these mechanisms cooperate, but their cooperation would lead to greater efficiency in the capture of food.

5. HOW DOES A SEPARATION BETWEEN USEFUL AND UNUSEFUL TAKE PLACE?

The next point is the selection of particles on their way from the gills to the mouth. Numerous details on the ciliary mechanism of the gills and mouth palps have been given for many species, see especially D. ATKINS in *Quart. J. Micr. Sc.* 1936-38. YONGE cites NELSON (1923 b) who concludes that feeding in the oyster is accomplished "through the delicate coordination of nervous, muscular, ciliary and mucous secreting elements in which mechanical sorting of the materials plays the most important part": "an admirable summary of the state of affairs".

The particles are divided by the movements of different kinds of cilia into two groups: one that is refused, the other that is accepted as food.

YONGE, in his first paper on this subject, dealing with the feeding of

the soft clam, *Mya arenaria*, supposed that the principle of this separation was based on weight of particles, not on size. His argument was that in the clam's stomach he found thin filamentous strips of algae up to 1 mm in length, though the largest solid particles (sand, etc.) were no more than $200\ \mu$ in diameter, and the majority no more than $20\ \mu$. YONGE seems to have dropped this supposition when studying the oyster. Though he is not quite clear on this point he considers from then on size of particles apparently more important than weight; I think, because he found that conglomerations of particles are rejected, though separate ones are carried to the mouth. This in itself is no evidence, of course, and I, personally, am not convinced that weight is unimportant. Perhaps, however, there is a combined principle of weight *and* size.

COE (1947) finds for the Pismo clam that more than half of the stomach-contents may consist of sand, the coarsest grains of which measure $200\text{--}300\ \mu$ longest diameter. That may mean that the sand coarser than that is refused. Thin fragments of periostracum and chitin, however, of nearly 1 mm in length and filamentous algae 1.5 mm long do also occur, they being the largest objects observed. He further finds that solitary diatoms of $50\text{--}200\ \mu$ and smaller are accepted, but colonial and spiny species are usually refused. I can only understand all these facts through the assumption that both weight and size play a rôle, but the matter remains uncertain.

The point, whether there is other selection than that according to weight and (or) size, for instance according to organic and inorganic particles, hardly appears to need consideration here, because nearly everyone now agrees that the latter selection is out of the question. In connection therewith the following should be mentioned, however. BULEY (1936) has stated that he found hardly anything but dinoflagellates in mussel stomachs, though in the sea water in which they lived he found very few. According to his counts the sea contained 2.4% of dinoflagellates and 97.6% of diatoms against the mussel stomachs 97.4% of dinoflagellates and 2.6% of diatoms. This would mean selection and it tallied with Fox' belief (1936) that dinoflagellates are valuable as food. In 1942 COE and Fox still cited these observations.

But from 1943 on Fox and COE came to the conclusion that dinoflagellates do not form a valuable food. Since then they no longer believe in selection and BULEY's observations are no longer mentioned (COE and Fox, 1944; COE, 1947). The possibility can probably not be excluded that in this case dinoflagellates may have exceeded diatoms in the bottom water, which reached the mussels, though in the higher layers diatoms exceeded dinoflagellates. — Also LOOSANOFF and ENGLE (p. 50–51) consider the possibility of selection, and their vision cannot be

neglected, because they had an enormous practical experience.¹ On the other hand, it is clear from such work as that of SAVAGE (1925) and others that there is a striking agreement between the composition of the plankton and that of the stomach contents of mollusks living in the water from which the plankton is taken, also in cases where much apparently undigestible material is taken in (oyster larvae for instance).²

The most important point in connection with the problem of selection is that of the influence of the concentration of the suspension pumped in. It was remarked already that even high concentrations may be pumped in, but this does not mean that they are favourable to the animals, anyhow, and that most of the material in question would be carried to the mouth. KELLOGG (1915) was of opinion "that a lamellibranch is able to feed only when waters are comparatively clear, when diatoms are brought to the gill surface a few at a time, and that in muddy waters, all suspended particles, of whatever nature, are led to outgoing tracts". This view has become the subject of much discussion (see LOOSANOFF and ENGLE, 1937) and DODGSON and others were cited (see DODGSON, p. 175), who in mussels found the largest quantities of faeces in the muddiest water; in other words, the food from this water had been ingested notwithstanding the high concentration of the silt. We may expect, however, that mussels may behave quite differently from oysters and that the different species of oysters behave by no means the same. In all kinds of animal groups we find species able to cope with large quantities of silt and others which cannot work the silt away, especially the sponges, anemones, corals, and hydroids embracing numerous instances. "ELSEY (1935) found that *O. gigas* withstands existence in turbid water much better than *O. lurida*, which closely resembles *O. edulis*" (LOOSANOFF and ENGLE, 1947). But LOOSANOFF and ENGLE even defend the view that through this cause scarcity of plankton may be better for oysters than its rich development and few biologists will probably accept this. Nevertheless the principle itself may be right.

If large quantities of silt or other suspended matter are pumped in they may clog the gills, so that oxygen intake may become difficult.

¹ SMIDT (1951, p. 111) refers to LOOSANOFF (1949), who "states that feeding *Ostrea* are capable of choosing between different flagellates".

² There is an interesting observation of DODGSON (p. 187), who describes how mussels in very hot weather, although open and discharging vigorous streams from their anal siphons and manufacturing pseudofaeces in large quantities, refused to ingest any of the suspended material through the mouth. "The water at the beginning of the experiments was 66° F, but rapidly rose, reaching 72° F in the course of an hour. A day or so later, the same mussels resumed their normal feeding in water at 64° F." But this is no instance of selection, of course.

Further, it must cost large amounts of mucus to work such quantities away. This may be sufficient reason for working the silt away along the shortest possible route, that of the pseudofaeces. Moreover, dense masses of small particles will easily clot together and then be dealt with as heavy or large particles, which are ejected as pseudofaeces. This was what KELLOGG (1915) meant and his viewpoint may be right.

LOOSANOFF and ENGLE conclude from their experiments with suspensions of micro-organisms of different concentrations that high concentrations in the oyster give many pseudofaeces and few faeces, and the reverse.¹ – COE and FOX (1944) say about the Californian mussel: "The excess, if not too great, may pass unchanged through the digestive system, but in case of a very great surplus most of the material is rejected by the palps and is discharged from the mantle cavity as pseudofaeces." – COE (1947) states that the matter pumped in is largely refused "in dense suspensions of micro-organisms, spermatozoa, ova, yolk or oil globules, or starch particles".

Because these statements agree there will be little doubt that they are right. Details on these observations have not been given, however, and one would like to know whether the statements are based on a general impression or on more. It is well known that concentrated suspensions produce large quantities of pseudofaeces, but this is only natural. In view of the fact, that there has been so much controversy on this point, it should be established beyond doubt that not only do the quantities of pseudofaeces on feeding of concentrated suspensions increase, but also the quantities of faeces decrease.

In connection with the problem of the refusal of material in the presence of concentrated suspensions the observations of DODGSON on the movements of a membrane in the inhalent opening of *Mytilus edulis* are of much interest; DODGSON gave it the name of velum. These observations form an extension of earlier ones of KELLOGG (1915) and ORTON (1912). KELLOGG was the first to suppose that the velum might have the function described below.

It is usually assumed that refusal of pumped in material is wholly due to the activity of the cilia of gills and palps, which carry the refused material to the place of ejection of pseudofaeces. DODGSON describes, however, how the velum is lowered when there is much suspended matter in the water, with the result that the current entering the inhalent opening is directed to the posterior part of the mantle margin, from where much material is discharged forthwith as pseudofaeces.

¹ The limit for high concentrations, in producing a high percentage of pseudofaeces, would differ for different micro-organisms, and LOOSANOFF and ENGLE remark that matters must become quite complicated when, as in nature, all kinds of organisms and material occur together.

The reader is referred to DODGSON's full description (p. 172-176) and figures of the velum for a right understanding of this fact.

It means that the mussel has more means than ciliary activity alone to dispose of excess matter and a similar state of affairs may hold for other bivalves (KELLOGG described the velum for *Schizothaerus*).

The question whether high concentrations would influence the velum movements both mechanically and chemically remains open. It was stated above already that high concentrations may have a chemical (toxic) effect on pumping and they might have a similar effect on the velum movements as well. Judging from DODGSON's description we are further allowed to assume that mechanical influences are important, anyhow.

DODGSON (p. 174) supposes that the velum not only functions in keeping excess of suspended matter from entering the inter-branchial spaces and anterior parts of the mantle cavity, and in facilitating their rejection in the recurrent marginal stream, but that it also exerts a certain selective function, the degree of diversion of suspended matter varying with its amount, and possibly with the size or irritating properties of the suspended particles (e.g., in the case of sharp sand grains, etc.).

6. WHAT PART OF THE MATERIAL RETAINED IS ACCEPTED, WHAT PART IS REJECTED?

Stomach contents have given us much insight into this question.

The stomach of *Mytilus californianus* and *Mytilus edulis* contain all kinds of phytoplankton (algal spores, dinoflagellates, small diatoms, other algae, and bacteria), zooplankton (flagellates, ciliates, other protozoa, spermatozoa and ova of invertebrates, etc.); further fine material which is considered detritus; and finally fine sand and shell material (FOX, 1936; COE and FOX, 1942; FOX and COE, 1943; COE and FOX, 1944; COE, 1945). COE (1947) finds for the Pismo clam, which occurs on sandy coasts, that more than half of the stomach contents may consist of sand. He further finds dinoflagellates in fair numbers: especially *Prorocentrum* (40-50 μ long), *Gymnodinium*, *Peridinium*, *Gonyaulax*, *Dinophysis*, and many others of 40-60 μ . Spherical algal cells of up to 100-300 μ diameter, slender multicellular algae of up to 600 μ , with longest filamentous algae of up to 1.5 mm. Crypto- and phyto-monadines and other flagellates. Diatoms of 50-200 μ long and smaller forms often in great numbers. "Other living cells include algal zoo-spores and the gametes of nearly all the invertebrates of the vicinity, including those of the clam itself." It certainly is an uncommon achievement of COE to distinguish all of them. - The stomach contents

of the soft clam, *Mya arenaria*, according to YONGE "consist of very finely divided particles of organic debris, sand and micro-organisms, e.g. diatoms, singly and in chains; Foraminifera; minute, probably larval, bivalves; ostracods and other microscopic Crustacea, with parts of larger specimens; spores and eggs of various kinds; sponge spicules, and spines of all sizes. The great mass of material consists of small sand grains".

Many data have been published on the stomach contents of oysters, for which the reader may be referred to detailed work like that of SAVAGE (1925).

It is evident from the numerous observations given that the stomachs of different species always more or less reflect what is found in the vicinity. One gets the impression that simply all material below a certain size is ingested. Even large quantities of sand are dealt with as if they had nutritional value, this simply being due to the simpleness of the selection mechanism. In connection therewith there is little reason to assume that organic detritus present in the water should not be ingested in the same way as fine sand and this is what certainly happens, as was shown by PETERSEN and BOYSEN JENSEN in 1911 already. SAVAGE came to the conclusion that more than 90 % of the food contained in the gut (stomach and intestinal tract) of the oysters he investigated consisted of organic detritus. This detritus has a certain food value to those organisms which can digest it. The point is, however, whether the different species of mollusks indeed can digest it, a problem, which is further dealt with below.

The stomach investigations, together with a direct study of the material that is rejected as pseudofaeces¹, give at the same time an impression of what is refused. COE (1947) says that among the dinoflagellates *Ceratium*, which are spiny and 200–300 μ long, are not ingested; diatoms of 50–200 μ long and smaller forms are often found in great numbers, but colonial and spiny species are usually refused. – Most sand above a certain grain size is certainly refused, but little is known about the actual grain sizes. Surely, larger pieces of detritus,

¹ The name pseudofaeces has been given to the refused material by DODGSON, to whose description and photographs of mussel-pseudofaeces is here referred. He already draws attention to the fact that their rejection "takes place at a point immediately posterior to the exhalant siphon – that is to say, at the apex of the arch formed by the fusion of the edges of the mantle folds". This means that they issue from the part of the inhalant opening next to the exhalant aperture (compare also Fox and COE, 1943, p. 233). DODGSON adds: "In virtue of the fact that this solid matter is mixed with a varying amount of mucoid secretion, it tends to be discharged in formed masses or strings, rather than in separate granules." Only in case the suspended matter is excessive do the pseudofaeces lose their coherent form. The resistance of pseudofaeces to disintegration according to DODGSON is striking. The reader is referred to his description on p. 162–164 for further details.

though they would represent much better food than fine sand, are rejected because of their size (weight). FOX and COE (1943) found that the pseudofaeces may also contain large micro-organisms, ova, larvae, etc. They say they "are usually returned to the sea while still in a living condition", but unpublished observations of KRISTENSEN point to the possibility that since they are enveloped in mucus they may partly die afterwards.

The quantities of pseudofaeces are large when the water contains much sand or many shell fragments (FOX and COE, 1943). They also depend, of course, on the total quantities of material pumped in; they are small when the water contains little matter in suspension.

In *Mytilus* the pseudofaeces simply drop beside the animal together with the true faeces, compare especially DODGSON's description. In other species they may be ejected with force. MAC GINITIE (1941) describes how the gaper clam, *Schizothaerus nuttallii*, ejects material by a sharp contraction of the adductor muscles, which quickly brings the valves together and squirts the water out through the incurrent siphon. This activity according to MAC GINITIE undoubtedly accounts for some of the squirting by clams on mud flats when the tide is going out. When the flats are nearly bare a considerable amount of sand and other material may have accumulated and this is rejected. Longnecked clams usually eject water much more forcibly than those with a short siphon; *Schizothaerus* squirts the water from 3 to 5 feet high. Squirting according to MAC GINITIE is also more frequent when the tide is first coming in. — We can observe this squirting regularly in *Cardium edule*. The water is ejected here up to some decimetres.

7. WHAT PART OF THE ACCEPTED MATERIAL IS REALLY DIGESTED?

Though the selection mechanism of lamellibranchs is complicated enough, it works according to a very simple principle: that of separation of material by weight or (and) size; with the result that such undigestible matter as sand enters in large quantities. One cannot therefore consider the stomach contents as representative of actual food.

Data on the food value of the material pumped in have been collected in the very first place by studying the action of digestive enzymes. Especially YONGE studied the oyster and he also examined the soft clam (*Mya arenaria*), GRAHAM the razor clam, FOX and MARKS (1936) the Californian mussel, COE (1947) gave some notes on the *Pismo* clam. These investigations all led to the result that amylase and glycogenase are produced in significant amounts in the style of the digestive tract, while the same polysaccharidases as well as disaccha-

ridases, proteases and lipases would be produced intracellularly. Coe (1947) further found in the Pismo clam a weak cellulase, apparently produced by the style.

The majority of investigators are therefore of opinion that digestion is largely intracellular and that only minute particles, especially plants, can be attacked. On the other hand, the minority are represented by a number of notable exceptions, among whom the MANSOURS rank first. Their work is chiefly concerned with some tropical species, especially *Tridacna*. They are of opinion that extracellular digestion is not to be neglected.

NELSON (1933) cites an instance in which an *Ostrea edulis* yielded 0.75 cm³ of stomach contents, consisting mostly of a free-living nematode (*Chromadora* sp.). Analysis showed 160 worms alive and active, 471 dead but intact, and 5842 partially or wholly disintegrated. Such and other cases (among others many data in SAVAGE, 1925, for the oyster, in publications of COE for other species) do not furnish direct evidence that such animals can be digested, but there is no reason to assume the contrary in view of the fact that after disintegration has started small particles can be attacked further. The uncertainty in this field is well demonstrated by the contents of KORRINGA's paper (1949).

Largely because of YONGE's influence the chief food of lamellibranchs has thus for a long time been considered to be chiefly represented by phytoplankton in the form of flagellates, small dinoflagellates and small diatoms, whereas there was much difference of opinion not only as to the value of multicellular animals, but also to that of detritus. Particles of detritus cannot be identified in the stomach, intestine or faeces with the same certainty as can diatoms, dinoflagellates, etc. None the less, ever since PETERSEN (1911) stressed the importance of detritus as food for lamellibranchs the latter has been considered of more or less importance by a number of investigators. None of them, however, have given themselves so much trouble to show what value detritus may have as food as FOX and COE. It therefore is to be deplored that a number of inaccuracies in the papers of the latter have detracted from the value of their results.

In short, the reasoning of COE and FOX is: the total quantity of food contained in dinoflagellates, diatoms, flagellates, bacteria, etc. is so small that a mussel pumping the year round would only capture a dry weight of them, comparable to one fifth of what it needs. Therefore, another source of food must play a rôle and since there is no other source of particles small enough for digestion than organic debris, the latter must be of much more importance than all these organisms together.

This reasoning is based on the number of litres a mussel pumps in the course of a year, the average content of dinoflagellates and other

organisms present in the water, their weight, and the gain in weight of the mussel within a year. Taken as a whole, this reasoning may be more or less correct (the same standpoint was apparently held by MOORE, 1913), but it loses through inexact argumentation.

In 1936 Fox holds the view that dinoflagellates are a very valuable source of food. He attempts to prove this by observations on their digestibility, and his findings tally with those of BULEY already cited, who finds that they are apparently especially selected. Still in 1942 COE and Fox hold the view that dinoflagellates are readily digested, but because of their small mass can be considered *one* of the principal food supplies only. In 1943 they come to the conclusion that dinoflagellates pass the digestive tract largely undigested and from then onward they no longer attach much value to them as food. This is most natural, but they neglect their former findings (those of BULEY included) without recanting them. This can only lead to confusion, for even when one reads their papers in the right order it is not easy to understand the true state of affairs. The difficulty is still enhanced by the fact that in Coe's papers it is not always easy to make out what are new facts and what old ones already dealt with in an earlier paper.

Fox and COE conclude that one large Californian mussel within a year may pump some 22,000 litres of sea water. Now, in 1943, they calculate that such a volume, if it contains 9570 specimens of the dinoflagellate *Prorocentrum micans* (measuring $30 \times 57 \mu$) per litre, contains 4.2 g of dry weight, or some 10 % of the mussel's annual gain in weight, if it could all be digested and directly changed into mussel weight. In 1944 they state that the years 1940-'43 gave averages of 10,000-55,000 dinoflagellates per litre. In these years, therefore, 22,000 litres must have contained some 4-23 grams dry weight of dinoflagellates, and one would think that these must have been at least of *some* value. But COE and Fox now say that the dinoflagellates occurred in such dense swarms that few may have been ingested, whereas the rest were possibly rejected as pseudofaeces. Since the ingested ones must have been largely undigestible, very little remained. This is a somewhat arbitrary argumentation.

A large part of the work of COE and Fox concentrates on a comparison of mussel growth in the sea and the number of organisms present in the water. This work has been continued for more than four years and an enormous amount of labour has been involved. Their observations on growth may serve as an example how such work should be carried out. No correspondence is found between mussel growth and the quantities of diatoms or bacteria, but they do find some correspondence between mussel growth and the dinoflagellate populations. Since, however, dinoflagellates, when very numerous, according to COE

and Fox are largely ejected as pseudofaeces, since they are largely undigestible, and since a four fold increase in abundance according to COE and FOX (1944) is associated with an increased growth rate of the mussels of only 42 per cent, the correlation does not in itself furnish evidence that dinoflagellates are important as food. It may show no more than that both mussels and dinoflagellates thrive under the same environmental conditions. This in itself is not impossible, but it is used as an argument for the value of detritus and as such it is without value. It is clear from the experiments of COE and FOX (1944) that high dinoflagellate figures correspond with rapid growth of mussels; COE and FOX have shown that the dry weight of the ingested dinoflagellates in periods that they are numerous must be very important also in relation to the annual gain in weight of the mussel; FOX (1936) has made it probable that dinoflagellates are at least partially digested. If, nevertheless, one wants to assume that dinoflagellates are unimportant as food and that detritus should be considered of much more value one should at least suppose that the dinoflagellates already during their maximum abundance produce so much detritus that the latter apparently causes an increased growth of mussels. This conclusion is the more obvious since COE and FOX themselves assume that increased mussel growth may coincide with the periods of propagation of *Balanus tintinnabulum* and other species because the latter may furnish detritus to the mussel. Even such a conclusion, however, somewhat neglects the possible value of the *living* dinoflagellates as food for the Californian mussel.

There may be little doubt that suspended organic detritus is one of the valuable sources of food for certain bivalves, as has been assumed by many ever since PETERSEN in 1911 emphatically drew attention to this possibility. SAVAGE (1925), who obtained a great practical experience by his research, found that his oysters had their stomachs and intestine filled with about 25-100 times more detritus than plankton (both counted by volume). He therefore (and also because of the work of JENSEN, 1914) was of opinion that detritus must be taken seriously into consideration as a source of food for oysters, but that "fattening" of oysters may be due to a great consumption of small diatoms. I think it is about this same opinion which is held by most specialists: that the best food for oysters probably is small diatoms, but that detritus may be quite valuable as a cheaper food of lesser value. If we want to prove this, a direct, experimental method seems indicated. This is no easy task. One cannot feed natural detritus, because it cannot be separated from the plankton. GAVARD, however, fed an artificial detritus, according to KORRINGA (1949) with very good results. - The value of detritus will certainly differ for different species,

I am inclined to suppose that it may be more valuable to the mussel than to the oyster. It is clear, however, that very few workers sufficiently command all facts collected in this field up till now; in this respect a critical revision of our present knowledge in this field, not for one, but for several species, would be of much value. WERNSTEDT's conclusion (1943), his experiments would indicate that the food value of detritus is only small, is certainly unjustified.¹

Some remarks should still be added on the times the ingested material needs to pass the intestinal tract, as they increase our insight into matters of digestion. They refer to oyster, mussel and cockle.

LOOSANOFF and NOMEJKO (1946) say that oysters kept in water of 20.0° C under laboratory conditions passed the particles of food through their entire digestive system in from 1 hour and 20 minutes to approximately 2 hours and 30 minutes.

As to the mussel, numerous observations have been given by DODGSON (p. 182-188), who experimented with "substances such as carmine, chalk, flour, Prussian blue, etc." It was found that material ingested at the mouth may appear at the anus within 1 ¼ hours. Moreover, an alimentary canal engorged from end to end may be completely evacuated in a similar period. "If open, and passing good siphon currents, they appear never to fail to ingest the suspension, but 3, 4, and even 6 hours have been observed to elapse before the passage of the index faeces. In the last case, however, the mussel had been stored for a week in one of the tanks, during the early part of which the weather was hot, prior to the experiment." And though a full tract may be emptied in 1 ¼ hour it may also need a longer time, up to several hours. — Observations of ZOBELL and FELTHAM (1938) gave results, which do not essentially differ from those of DODGSON. They found that bacteria disappeared from the intestinal tract of mussels within six hours after being fed. Their mussel was *Mytilus californianus*.

Finally, JØRGENSEN (1949) found that 30-60 minutes after the pre-

¹ WERNSTEDT worked with *Cardium edule* and *Macoma baltica* and his conclusion could only hold for these species. It is probable, however, that the value of detritus for a detritus feeder like *Macoma baltica* cannot be small. His experiments are insufficient to prove or disprove this.

The value of detritus must be quite different to different species of one and the same animal group. Among crabs many species certainly cannot make use of detritus, whereas others, e.g. the tropical *Uca* species and *Eupagurus bernhardus*, feed on hardly anything else. That the latter species should have such food seems to follow from the fact that it prefers rotten meat (for instance, that of fish) over fresh meat. Such detritus feeders are to be found in many animal groups. This fact is not at all new, of course, but it should constantly be kept in mind to make one realize that it is not the small food value of detritus, which makes detritus valueless to some animals, but the impossibility of such animals to use detritus for food (for the food value of detritus see BOYSEN JENSEN, 1914).

sensation of graphite suspension to mussels large amounts of graphite faeces were ejected through the exhalant siphon. Since JÖRGENSEN worked with rather young *Mytilus edulis*, his observations, again, are more or less in agreement with those of DODGSON. – In all these cases undigestible or presumably easily digestible matter was used and the times it needs to pass the intestinal tract is short.

It follows from the observations of AUSTIN on the stages of digestion of stomach contents of mussels at various times after feeding natural food that digestion had commenced one hour after feeding, but that more than five hours elapse before diatoms in the stomach may have lost their chlorophyll and that the skeletons of diatoms and dinoflagellates were still present 24 hours after the diatoms had been fed. This probably shows that slowly digestible matter passes the tract much slower than undigestible or presumably easily digestible material. The observations of COE (1945) apparently show the same. "That minute diatoms are readily digested is shown by the fact that within 20 hours after the mussels have been fed cultures of small species the faeces consist mainly of chloroplasts, with only a few intact cells." COE considers this a short time, but it is long compared with the other times mentioned.

Finally, the data of Fox and COE (1943) show that mussels brought from the sea into the laboratory may give off undiminished quantities of faeces for three succeeding days. Only after the fourth day the quantity decreases. This means that it takes several days for a tract filled with natural food to lose all its material. In this connection it should not be forgotten that *Mytilus californianus* is a very large species.

As to the cockle I am acquainted with one observation only, that of DAMAS. He says the following. "L'activité nutritive de ces *Cardium* est en effet énorme. Des individus tenus en état d'inanition prolongée et dont le tube digestif vide ne fournissait plus d'excréments reprennent la reproduction de boudins après 12 minutes si on les replace dans une eau vaseuse. Il ne faut donc à la nourriture que ce laps de temps pour parcourir le tube digestif tout entier." It is not probable that real food would need such a short time and it would be of interest to pay some attention to this point.

8. WHAT IS KNOWN ABOUT THE QUANTITY AND COMPOSITION OF THE FAECES?

Generally speaking, the faeces of mollusks are excreted in the form of pellets, the size and form of which are different for different species, compare especially MOORE (1931 a, b, and c, and 1939). They are large and long in the mussel (for description see DODGSON, 1928, p.

161-162) and small and more or less globular in the cockle. MOORE (1939) says that "in general, carnivorous animals tend to produce faeces of loose consistency, vegetable eaters firmer ones, and deposit eaters (like our lamellibranchs) the most resistant of all." "The pellets of deposit eaters will stand (MOORE, 1931a) fairly rough handling, and can even be boiled with sulphuric acid or strong caustic soda without breaking down." MOORE (1931a) found them in bottom deposits, at least a hundred years old and they showed no evidence of breakdown. He ascribes their resistency to the high mineral content of the food of the animals producing them and considers it probable that progressive glauconization may cement and strengthen the pellets so that they may well be preserved permanently (MOORE, 1939).

The quantity of faecal pellets produced is more or less known for cockles. DAMAS counted one pellet issuing every 8 seconds. That would make 10,800 pellets a day. According to DAMAS their size is 0.3 mm^3 and the animals therefore would produce 3240 mm^3 of faecal matter a day.

Counts in July, 1949, on the sands in front of the Zoological Station, Den Helder, gave the following results:

Number of counts	Extremes of lapse of time between two successive pellets (in seconds)	Average lapse of time between two pellets (in seconds)
± 8	14-23	19
± 8	7-20	12
4	8-27	19
2	13-14	14
8	14-23	19
5	6-37	18
17	8-32	15
21	10-40	27
4	9-16	12
12	10-97	23
Total ± 89		Average 18

These observations show that a total of about 90 observations on 10 different animals gave on an average one pellet every 18 seconds. This was in the middle of summer. It may be assumed that the number is perhaps higher in spring, but certainly much lower in winter, so that 40 seconds may be considered a better average for the year than 20. The *Cardium* had been born in 1947, they were two years old and measured about 30 mm. Older animals may work slower than young ones and DAMAS may have observed younger cockles. The figures show that there is much individual variation.

It should be added that one cockle, after having given off 8 pellets with lapses of time of 14–23 seconds, retained all material for 450 seconds and then gave off a complete string of pellets. There then was a pause of another 60 seconds, thereafter about the old rhythm was taken up again.

If the faecal pellets of cockles of the size mentioned would have a size of 0.3 mm^3 as given by DAMAS and if these cockles would produce one pellet every 40 seconds they would produce 648 mm^3 of wet faecal matter per day. As their specific weight is somewhat higher than that of sea water their wet weight must be some 648 mg at the least.

For the mussel similar observations are not available, but FOX and COE (1943) have determined the dry weight of faeces given off by individuals of different length and they find 7.5, 45, 95, 176, and 281 mg dry weight a day for mussels of 20, 40, 60, 80, and 120 mm length. If I understand them correctly, however, they have decanted part of the sand before drying and weighing the material, so that all these values would be too low. – Also BLEGVAD (1915) gave some values. They refer to the quantity of faeces, produced by 100 g *Mytilus edulis* during 24 hours. The animals were apparently brought from the sea into an aquarium again and faeces and pseudofaeces were probably measured as one. Since, however, the production of faeces in the aquarium will continue and that of pseudofaeces will stop within a short time because new food is not available, most of the material produced must be true faeces.¹ 100 g mussels produced in one case 1870, in another 3080 mg (dry weight) of material. BLEGVAD does not mention the size of his mussels, but if they were large they would represent 2–3 animals, so that one large mussel would produce 800–1200 mg (dry weight) of matter per day. Since part of it may have been pseudofaeces, the faeces may have weighed maximally some 1000 mg (dry weight) per animal per 24 hours.

Finally, KAMPS made exact measurements of the quantities of suspended material laid down by mussels along the coast of the province of Groningen in the Netherlands. He used small boxes with 80 mussels each and control boxes with similar mussels filled with concrete. The water had free passage through the walls. The boxes were laid out in the sea and they were controlled every fortnight from March to November. It should be added that the water along the coast of Groningen contains several times more suspended matter than that in the western part of the Waddensea, where the work of the Zoological

¹ It is not wholly correct to consider the quantities mentioned as representative for 24 hours, because the mussels were taken from the sea and their faeces collected over the first 24 hours when they got no food. According to the observations of FOX and COE, however, mussels taken from the sea may give off undiminished quantities of faeces for 3 successive days.

Station was mostly carried out. KAMPS, who permits me to mention his results (see also KAMPS, 1950, p. 112), found that 80 large mussels within 2 weeks produced quantities ranging from 2600 to 4200 g, with an average of about 3300 (13 determinations). This gives an average production of about 3000 mg (dry weight) per large mussel per day, a quantity 3 times that found by BLEGVAD, but including both faeces and pseudofaeces. The relation between pseudofaeces and faeces within that amount is not known, but a large part of the material may represent pseudofaeces and it is assumed that the true faeces did not exceed 2000 mg per large animal per day at the very most. Assuming a water content of the faeces of about 75 % the wet weight would be some 8 g per large mussel per day, i.e. some 9 times more than that found for the cockles near Den Helder. It should be added once more that the figure is certainly very high and that a faeces-production of half that amount may be more normal.¹

FOX and COE (1943) determined also the composition of mussel faeces. Here, again, however, "as much sand and shell as possible was separated by comminution and subsequent decantation from the samples at each collection". Apparently, this sand is not contained in the results of their analysis. They find some 70 % of ash ("chiefly sand and shell"), somewhat more than 1 % of N and some 0.5 % of PO_4 . If, as assumed, the decanted sand was not calculated, the true ash figures become higher. COE (1945), basing himself on these figures of FOX and COE (1943), says that mussel faeces consist for some 30 % of organic matter, but this quantity would become lower.

TAKAHASHI and YAGI (see MOORE, 1939) found 0.21–0.42 % of P_2O_5 , i.e. 0.28–0.55 % of PO_4 in recent faecal pellets²; this value is not much different from that of FOX and COE. – FOX and COE multiply their nitrogen figures by 6.25 – "commonly accepted as applying to the

¹ Assuming that the animals pumped 1.8 litres per hour for no less than 20 out of the 24 hours the water pumped must have contained more than 83 mg dry weight of suspended matter per litre plus the quantity digested, a total of at least 100 mg per litre. If they pumped for shorter periods or if they pumped smaller quantities per hour the quantity of suspended material present in the water must have been still greater. The quantities are therefore at least 4–5 times greater than those in the western Waddensea according to POSTMA's determinations. This is in agreement with direct measurements of the quantities of suspended matter per litre, as carried out in the eastern Waddensea by KAMPS. Nevertheless, the mussels (and also the cockles) in the eastern part of the Waddensea remain small. As the salinity of the water there is as high or higher than that in the western part the composition of the suspended material may be less optimal in the eastern than in the western part. In this connection the question of the possibly adverse influence of concentrated suspensions (p. 203–204) is of much interest.

² The phosphate content seems to increase as a result of fossilisation; MOORE found values of up to 30.7 % P_2O_5 in old layers.

proteins of marine origin", and thus obtain some 7 % for the protein content. This value would also become lower.

It is well known that lamellibranch faeces may contain fair quantities of undigested (partly even living) organisms. These have therefore passed the digestive tract undamaged. It is generally assumed that their presence is due to the absence of enzymes which can attack them. NELSON (1933) is of opinion that in the oyster they are the result of the incomplete separation of food particles from undigestible matter, inherent to the feeding mechanism. COE and FOX, however, in most instances ascribe their presence to excess of food (COE and FOX, 1942; FOX and COE, 1943; COE and FOX, 1944; COE, 1945, and 1947), an opinion apparently going back to FOX (1936). Even after their discovery (FOX and COE, 1943) that so many dinoflagellates remain undigested they ascribed this at first to overabundance of food. Only in 1944 (or later) did they mention incomplete attack through the absence of the right enzymes as a possible cause. But overabundance of food was still held to be the chief reason for unattacked material in the faeces in other instances even now.

The descriptions of COE and FOX (see especially FOX and COE, 1943, p. 232) make the impression on me that excess of food may indeed lead to large numbers of unattacked organisms in the faeces. "When algal zoospores are abundant the phagocytic cells of the digestive diverticula are distended with these reproductive cells. At such times they also form the principal constituent of the faeces, since the mussel is able to assimilate only a small proportion of the vast numbers ingested." The same impression is given, for instance, by the description of LOOSANOFF and ENGLE (1947).

If, however, living or undamaged organisms in the faeces can be due to two different causes: overabundance of food (eventually due to increased incomplete separation as meant by NELSON) as well as inability to attack the food, their presence in the faeces can no longer be used as evidence that the right enzymes for their digestion are wanting. In the experiments of LOOSANOFF and ENGLE high concentrations of micro-organisms produced large quantities of pseudofaeces as well as large numbers of living organisms in the faeces. It has been suggested that these organisms may have been partly unsuitable as food. If they may have been due to overfeeding the supposition that the food was unsuitable may be wrong. The most we can say at present apparently is that in certain cases we see digestion fail to break down the food.



Fig. 6. Western part of the Waddensea west of the watershed between the island of Terschelling and the coast of the province of Friesland. Dotted areas represent the sands falling dry at lowest low water of spring tide.

V. THE ACTIVITY OF COCKLES AND MUSSELS WITHIN THE WADDENSEA

The mollusks of the Waddensea may cause changes to their environment in two ways: first, by changing the geomorphological aspect of the whole, secondly, through their influence on the character of the material from which the area is built up.

The firstnamed influence, that on the geomorphological aspect, can only be small. The general morphology of the Waddensea, with its configuration of main channels and wide flat areas, is in no way dependent on the presence of mollusks, and the influence of the latter is only quite secondary and relates to morphological details. In fact, I am acquainted with one good instance of such an influence only. Where mussel beds develop over the drainage channels of large shallows the course of these creeks can be changed under the influence of such beds as it may also change through accumulation of sand. For the configuration of the Wadden as a whole this fact is of quite secondary importance, of course.

One may ask whether the creeks did not rather develop as a result of the presence of mussels instead of the mussels as a result of the presence of creeks. This is not the case. The large flats possess a number of drains. Many of these are favourable as a habitat for mussels, which may form a dam of beds across and a series of beds along them. In growing heavier the dam becomes an obstacle to the current and the water partly begins to flow around the dam so that a new creek is developed. This new creek results from the presence of mussels; yet, one cannot say that the creek owes its existence to them, as in a somewhat different form it was there already before the mussels came.

The second way in which mollusks cause a change in the whole is that they alter the character of the substratum. In this respect the animals may be of importance in two ways: by altering the quantity, composition and structure of the bottom material, and by the accumulation of lime in their shells. Having ascertained in the foregoing chapter the details necessary for a correct understanding of the conversion of suspended material into faeces and pseudofaeces we may now see of what importance the activity of these mollusks is in these respects.

I. THE ACTIVITY OF THE COCKLE

According to WILLEMSSEN's observations dealt with above a cockle of two years old pumps about 0.5 litres of water per hour. Assuming that the average time of pumping per day for the cockle may be comparable to that of oyster and mussel, the value of 20 hours found for the latter species may be taken as a suitable mean for submerged cockles. Since

the quantities of water pumped, however, may decrease at low temperatures and cockles may fall dry a certain period every tide the average number of hours of pumping per day is here estimated at 12, this presumably representing a very low figure.

The water of the Waddensea according to POSTMA's determinations contains on an average some 25 mg (dry weight) of suspended material (including plankton) per litre. During windy weather the quantity increases. On the other hand, it may be especially low over the sands where the cockles are living, since the water layer is rather easily depleted there. The mean figure for the water of the Waddensea as a whole may therefore be lower, and 20 instead of 25 mg is therefore taken as a starting point. As very little material is refused at the siphon entrance, practically the whole of this material is fixed in the form of flesh, energy, faeces or pseudofaeces.

A cockle pumping 12 hours a day at a rate of 0.5 litres an hour may fix, then, some 120 mg per day or 43.800 mg a year.

Part of this material is digested, part is rejected as pseudofaeces, another part is returned as faeces. It was stated above already that one faecal pellet issuing every 40 seconds may be considered a low average. That makes per day of 12 hours 1080 and per year 394.200 pellets. DAMAS estimates the volume of one pellet at 0.3 mm^3 . His cockles may have been smaller than ours, but the same figure will be used here. That comes to 118.260 mm^3 of pellets a year. I conclude from MOORE's paper (1931a) that the water content of this material is some 85 %, expressed by volume. Assuming a specific weight of somewhat more than 1 (the pellets are heavier than the sea water) their dry weight would be at least 17.000 mg.¹

If the above assumptions should more or less hold good one cockle in the course of a year would take in and fix at least 44.000 mg (dry weight) of suspended matter (plankton included) and reject at least some 17.000 mg of faeces.

The difference between these two figures would represent materials for the cockle's gain in weight, and for its sexual products, the energy for its metabolism, and its pseudofaeces.

According to our calculations the dry weight of the organic material makes about 12 % of the total dry weight of plankton and suspended matter. The 44000 mg pumped in may therefore contain some 5000 mg (dry weight) of organic material

¹ It makes much difference whether the percentage of the water is expressed per volume or per weight. MOORE expresses the water content per volume, HÄNTZSCH (citing STOCKFISH and BENADE) by weight. Weight figures are much lower than the corresponding volume figures, how much depends on the relative proportion of sand and other material. If the faecal pellets consist for 50 % of their volume of sand with a specific weight of 2.5, and the other 50 % are clay, organic material and water, with a specific weight of about 1, their specific weight is about 1.3 and the dry weight here calculated then becomes about 23000 mg.

and this is divided over the pseudofaeces, the food that is taken up, and the faeces. Because nothing is known for certain about the average percentage of organic material within the pseudofaeces and faeces it is impossible to say what percentage of the material is actually digested. Should some 1200 mg be contained in the pseudofaeces, some 1800 mg be digested and as much as 2000 mg make part of the faeces, the latter would contain some 12 % of organic matter. Should occasionally as much as 3000 mg of the organic material make part of the faeces the percentage of organic matter within the latter would amount to 17.5. These figures differ so much from the 30 % mentioned by Fox and Coe (1943) for the Californian mussel, that in themselves they form an argument against the usefulness of their figure which – it be remembered – was acquired after decantation of the sand. We are very far, however, from being able to give a provisional metabolic balance sheet of the cockle, as Fox and Coe have so admirably attempted to do for the mussel.¹

If one wants to judge the influence of the cockle population on the fixation of suspended matter in the Waddensea as a whole the number of cockles should be known. It is difficult to estimate the average number of *Cardium* per square metre of sands since there are – as already described – stretches with 2000 adult individuals and also sands (around the island of Griend for instance) with very few or even none. In order not to arrive at too high an estimate 10 cockles per square metre will be taken as an average.

N. Pijl, analyst to the Zoological Station, has determined the total surface of the western part of the Waddensea west of the watershed between Terschelling and the Friesian coast. It amounts to about 1557 km². About 600 km² (38 % of the total) fall dry during the lowest low waters of spring tides and this is about the area inhabited by the cockle. These 600 square kilometers may therefore be inhabited by a total of at the very least some 6000 million adult cockles, but twice that figure is probably more correct.

As one adult cockle would pump in and fix some 44.000 mg (dry weight) of suspended material in the course of a year 6000 million cockles would fix 264 million kg (dry weight) of suspended matter. Assuming a water content of 75 % (by weight) the wet weight may amount to 1000 million kg or a volume of some one million cubic metres.

These same cockles would produce at least some $6 \times 10^9 \times 17.000$ mg dry weight of faeces a year. This makes some 100 million kg. Expressed in volume units they would produce (see above) some $6 \times 10^9 \times 118.260$ mm³ or some 0.71 million cubic metres of faecal pellets a year.

¹ The above percentages of organic matter (12 % in the material pumped in and perhaps 12 % in the material ejected) both relate to the dry weight at 120° C. They are not comparable, however, since through ejection of sand with the pseudofaeces the percentage of organic material in the stomach contents will first become higher than 12 % and then decrease again to for instance 12 % in the faeces.

This amount may be assumed to be spread over an area of 600 km². It thus would form a layer of some 0.12 mm high. Should the average number of cockles per square metre be 20 instead of 10 (a possibility which may be nearer the truth) the annual layer would be some 0.24 mm. Its thickness would gradually decrease through water loss. It follows from numerous values obtained by J. SCHEELE for the harbour of Ymuiden that the water content of its bottom sediment may decrease from above 70 % by weight (some 86 % by volume) to 60 or even 50 % (some 72 % by volume) towards 1 m depth. MOORE finds a decrease from about 85 to about 77 % (by volume) for the deeper layers of the Clyde mud, which according to him are some 5–25 years old. Such a decrease would cause a decrease of the thickness of the annual layer of 0.12 to about 0.10 mm.

To the volume and weight of the faecal material must be added that of the shells. The shells of 100 well grown Waddensea cockles of about two years old weigh some 750 grams. This means that the lime production of one cockle per year may amount to something like 3–4 g and that 6×10^9 cockles produce some 18–24 million kg of shells. 2000 cockle shells of the above size occupy a volume of about 0.01 m³. If it is assumed that 10 cockles of two years old grow up on a square metre of flat every 2 years, they produce a layer of lime of some 0.025 mm. The layer of faeces would therefore have more than four times the thickness of the layer of lime. The layer of faecal material would contain much water, however. – To this layer of faeces and shells must be added the pseudofaecal material, the quantities of which are difficult to estimate through want of data.

In reality, the assumption that a layer of faeces would be spread over an area of 600 square kilometers of sands is untrue, since the pellets are probably largely transported to the creeks and through them to quiet areas.

Part of the shells are carried to the creeks, but many (I think most) flats show dense layers of cockles, clams and mussels at some depth below the surface and these must be of some influence on the growth of the flats. Where the quantity of sand available for building should be small, shells cannot be without some importance. It is true, they are partly dissolved again through the action of carbon dioxide, especially in a bottom rich in organic matter, but this is a very slow process and it certainly stops after some time, because there is so much lime in comparison to the quantity of organic material.

The combined effect of the activity of 6000 million cockles in the western part of the Waddensea would be that they withdraw from the water one million cubic metres of wet or some 264 million kg of dry suspended matter (plankton included); that they produce something

like 0.7 million cubic metres or some 100 million kg (dry weight) of faecal material and a quantity of pseudofaeces that is at present difficult to estimate. Further, the amount of shells produced by 6000 million cockles must amount to some 18–24 million kg or some 18–24 thousand cubic metres. Assuming that at least 90 % of this material is CaCO_3 the lime production amounts to some 16–22 million kg. Shells, faeces and pseudofaeces together may represent at the very least some 140 million kg dry weight and a wet volume of some 0.85 million cubic metres.

All figures here given represent minima, as they are based on low estimates. It is well possible that they must be doubled. It is improbable, however, that they should be thrice as high as here given.

DAMAS (1934) came to the conclusion that the quantities of mud deposited in the neighbourhood of Zeebrugge would amount to one and a quarter million cubic metres per year. His estimates were based on one faecal pellet issuing every 8 (instead of 40) seconds and 1000 (instead of 10) cockles per square metre over an area of 250 hectare or 2.5 square kilometres. This would mean that an area 240 times smaller than the western part of the Waddensea would produce nearly double the quantity of 0.7 million cubic metres calculated for the latter. Though this seems a rather high estimate the fact need not be quite impossible, because everything depends on the density of the population. The estimate of 1000 cockles per square metre for the Waddensea would be much too high, for though there are stretches with 2000 fullgrown cockles per square metre the extensive sands with only a few per m^2 reduce the average.

2. THE ACTIVITY OF THE MUSSEL

Before proceeding in order to see what may be the final conclusion as to the general importance of the above facts the mussel should be dealt with.

The chief difficulty in the mussel is to make a more or less trustworthy estimate of the number of individuals. It is not so difficult roughly to estimate the number of cockles present in the area under consideration, because they are restricted to the flats and fairly regularly distributed there. The population, moreover, is often restricted to one single year class, so that the estimation of the number of old individuals is little disturbed through the influence of large numbers of younger animals. With the mussel matters are quite different. They are not restricted to the flats, but occur also within and along the creeks. The largest bank occurring in the Waddensea in the years 1945–'50 was about 3 kilometres long, about 1 kilometre broad, and it

was lying about 4 metres deep. How many mussels may inhabit such a bank? Moreover, one always finds large numbers of younger and older mussels in the same area at the same time.

For these reasons another method has been followed here for estimating numbers, namely that of using the results of the fisheries. This would not have been possible without the help of Dr B. HAVINGA, director of the Institution for fisheries research, Amsterdam, the fisheries inspector, Mr VAN HENGEL at Amsterdam, and the fisheries surveyor, Mr DE VLIETTER at Den Helder.

In 1949 2.280.000 kg of consumption mussels were fished in the western part of the Waddensea studied here. These are mussels of about 6–8 cm length. As 1 kg contains about 25 specimens their total number may have been some 57 million individuals. To this figure must be added some 271.000 kg of mussels, "cultivated" south of Terschelling and near Griend. They represent some 6.8 million individuals and bring the total at 63.8 million.

Further, some 9.563.000 kg of smaller mussels, of about 3–6 cm length, were fished. They are used as food for ducks and about 50 of them are contained in 1 kg, so that the number of individuals may have been 478 million.

Finally, some 3 million kg of young mussels (so called seed) were fished. One kg of these according to PIJL contains some 500 specimens of from 5 to 30 mm length and the total number of individuals may have been 1500 million.

Now, DE VLIETTER, who is better acquainted with the Waddensea than anyone else, is of opinion that the total fished in 1949 represents about one third of the total present. He believes that the catch consisted of less than half the total and that it was certainly more than one fourth. In other words, the Waddensea in 1949 would have contained some 191.4 (say 200) million consumption mussels, some 1434 (say 1500) million halfgrown mussels, and some 4500 million small mussels.

As 1949, however, was a very good year, these figures should not be considered averages, and one third is therefore taken here. That gives some 70 million old, some 500 million halfgrown, and some 1500 million young mussels of about one year old.

The mean quantities of water pumped by the individuals of these three different groups (see p. 194) will be estimated at 1.5, 1., and 0.1 litres per hour pumping. It may again be assumed that the animals pump 12 hours a day and that they take in practically the whole of the suspended material, which will be estimated again at 20 mg.

The animals of group I then pump in: 70×10^6 (number of mussels) $\times 12$ (hours) $\times 1.5$ (litres $\times 365$ (days) $\times 20$ (mg) = 91.980×10^8 mg = 9.2 million kg of suspended matter.

The animals of group II pump in: $500 \times 10^6 \times 12 \times 1.- \times 365 \times 20 = 43.8$ million kg.

The animals of group III, finally, pump in: $1500 \times 10^6 \times 12 \times 0.1 \times 365 \times 20 = 13.14$ million kg.

So that the combined mussels of the western part of the Waddensea, which are estimated at 2000 million individuals, would annually withdraw from the water a total of some 66 million kg of suspended material.

Should the relation between the quantity of suspended matter pumped in and the quantity of faeces produced, and also the water content of the faeces, be the same as in the cockle, the mussels would

produce $\frac{100}{264} \times 66 = 25$ million kg (dry weight) of faeces or some 0.18

million cubic metres. If, however, a faeces production of 1000 mg dry weight per large animal per day is taken as a starting point (compare p. 214-215), the quantity of faeces produced by the large mussels alone (say 70 million individuals) is already 25 million kg. Since the quantity of material pumped in by all mussels together is supposed to be about 7 times the quantity pumped in by the large mussels the quantity of faeces produced by all mussels together would also be 7 times the quantity produced by the large animals alone, i.e. 175 million kg (dry weight). The great difference between the first and the last figure (25 and 175 million kg respectively) must be due to the fact that in the first calculation 12 hours of pumping per day and 20 mg of suspended matter per litre of water pumped were taken as a starting point, in the second case a *faeces*-production of 1000 mg for 365 days per year. It may be assumed that the former value is rather low, whereas the latter for the western Waddensea is certainly too high. It was stated already that conditions in the eastern Waddensea differ much from those in the western and they will probably differ much even at neighbouring places. Nevertheless, the figure of 25 million kg as an average for the annual faeces-production by mussels in the western part of the Waddensea will be maintained here.

The weight of the shells of the 2000 million mussels may represent some 4.7 million kg. This figure has been obtained by assuming that the average weight of the shells of the individual mussels of groups I, II and III may respectively be 10, 5, and 1 g.

3. THE ACTIVITIES OF COCKLES AND MUSSELS COMPARED AND COMBINED

Before proceeding, the figures found for the mussel should be compared with the corresponding ones for the cockle.

It has been supposed that the western part of the Waddensea, west of the watershed between Terschelling and the Friesian coast, on an average would contain 6000 million cockles and some 2000 million mussels, both estimates certainly representing rather low figures. The 6000 million cockles would withdraw from the water some 264 million kg (dry weight) of suspended matter. The 2000 million mussels would withdraw some 66 million kg. Cockle and mussel activity in the western Waddensea would therefore be related as 4:1.

It is assumed that the quantities of faeces and pseudofaeces produced by cockles and mussels show a similar relation.

The weight of the shells of 6000 million adult cockles may be estimated at about 21 million kg. The weight of the shells of the 2000 million mussels may represent some 4.7 million kg. This would contain that the cockles produce 4-5 times more shell weight per year than the mussels.

Adding the values for cockles and mussels these animals in the western Waddensea would annually withdraw from the water some 330 million kg dry weight of suspended matter (plankton included), representing some 1.3 million cubic metres of wet material. A very large part of this material, say two thirds at the very least, will be converted into faeces and pseudofaeces. Further, the animals would annually produce some 25 million kg of shells. Shells, faeces and pseudofaeces may at the very least represent some 250 million kg (dry weight) of material, which is not easily carried away.

It has been described above how the mussels, contrary to the cockles, occur in beds, where many thousands of individuals may occur together. The faeces and pseudofaeces of all these animals fall between and around them, filling all interspaces. The mussels are gradually covered by them, and they work themselves out of the sediment where this is possible. Part of them die and form a firm hold for others and they thus build a bank of silt and shells, the upper surface of which is covered by the living animals. The accumulations of silt in large beds may take enormous proportions. It is a general belief among mussel fishers that the layer of silt may reach a height of several decimetres within a year, and this is certainly true.

The reason why this material largely remains where it is produced and, contrary to what is the case in cockles, is only partially carried away, may be found in the form of the faecal bands, which are long, and also heavy (for figures see DODGSON, 1928; MOORE, 1931b; SCHWARZ, 1932). One also gets the impression, however, that the mussel produces more mucus than the cockle, so that the material adheres more firmly. Finally, the faeces can be carried away less easily, because they fall *between* the animals and are not ejected on sand as

are cockle pellets. Nevertheless, large quantities of this material are carried to the lee of the beds, where they may form extensive patches of a very soft sediment. Where dams of mussel beds cross the drains of large shallows this lee seems always to lie at the side of the beds turned away from the shallows.

When the musselbeds are broken up one regularly finds on these sites banks of a very consistent material, which has the appearance of clay and certainly contains a high percentage of the latter. These banks or patches are interspersed with shells. They are not easily destroyed and in musseldams across important drains one may find a number of such patches keeping stand in strong currents.

The difference in sedimentation between cockles and mussels, then, is that the cockles are regularly distributed and therefore produce pellets over wide areas, from where they are easily carried to the creeks; whereas mussels are distributed quite irregularly and produce their faeces locally; these faeces are not so easily carried away. The photographs given by SCHWARZ (1932, fig. 1-4) can well serve to illustrate the differences in question.

What, now, is the result of this combined activity of cockles and mussels?

That they annually convert more (perhaps much more) than 330 million kg (dry weight) of suspended matter into pseudofaeces, flesh and faeces and thus contribute to the fixation of the suspended material on a large scale. In this connection especially the great resistance of the faeces to disintegration is of much interest. MOORE (1931 a and b) has drawn attention to their long life. He found them in the Clyde area unattacked in muds of a century old. They may live shorter in shallow areas, where they are easier attacked, but even here their life may be very long. MOORE (1931) already drew attention to the fact that, biologically, the process of fixing the unconsumable remains into a form, which is unfit for further use, may be very important. Such species as cockles and mussels, which feed by pumping the water, and which must pump constantly so to speak, because their food gaining mechanism works according to a very simple principle and rather inefficiently (an idea especially expressed by FOX and COE), would be in a very adverse position if the water were to contain all the food remains of their neighbours. The "disadvantage" (if we are allowed to use such a word here), however, is that part of the organic material is fixed and therefore withdrawn from the cycle for a very long time. It is shunted on a side line so to speak, from where it may return after many years.

The result is that a large part of the material lies constantly unused. We found that the combined populations of cockles and mussels at least pump some 330 million kg (dry weight) of suspended matter

annually, containing some 12% or some 40 million kg of organic material. Should our former supposition (p. 219-220) hold good that up to two fifths of this material would be excreted within the faecal pellets about 16 million kg would be fixed in the latter per year. If they would resist disintegration for 25 years their deposit would contain some 400 million kg of organic material. Assuming that the other three fifths, or 24 million kg, contained in pseudofaeces and animal flesh, would have an average life cycle of at the very most three years, their total should be about 70 million kg. The value of such figures is very restricted, of course, but they may emphasize the fact that the depot lying unused for long periods may indeed be very important. Within this long period much of the material will, moreover, have a chance to be carried from the western part of the Waddensea to the eastern, whereas accumulation of this material in quiet parts may withdraw it from the cycle for much longer periods or even for ever.

Before leaving this chapter one would like to deal with the question of what influence cockles and mussels are on sedimentation within the Waddensea generally. We found it must be assumed that material in suspension is constantly carried from the North Sea to the Waddensea, where it is retained through sedimentation. To this process of retaining material cockles and mussels contribute on a large scale. The difficulty, however, is to compare this scale with that of the whole. At present, it seems hardly possible to say anything definite on the point, but the question deserves much attention.

VI. THE SOURCE OF THE ORGANIC MATERIAL

The question is of much interest what may be the chief source of the organic matter, which forms the base for the activity of these millions of animals. What may be the relation between the quantities of organic matter present in the Waddensea itself and brought to the latter from outside? Though a decisive answer to this question cannot be given, some general considerations may be of value.

Two processes are at work. One is concerned with the life cycle of the organic material within the area dealt with, the other with the interchange of material between the Waddensea and the surrounding waters. Though these processes cannot be separated, they will be dealt with one after the other.

Assuming, first, that the Waddensea would be self-supporting and received no material from outside (which is not the case, of course), the Waddensea could be treated as if it were a closed body of water. This closed body, then, would contain 6×10^9 cockles, pumping at

least 12 hours a day 0.5 litres per hour, i.e. 0.036 km^3 a day. The data, already given for the mussels, show that the adult mussels would pump 0.00096 km^3 , the halfgrown ones 0.00225 km^3 , the young ones 0.00135 km^3 a day. The total quantity of water, pumped by cockles and mussels of the western Waddensea, would amount, then, to 0.041 km^3 a day.

According to determinations of N. PIJL and H. POSTMA the mean depth of the Waddensea west of the watershed Terschelling-Friesian coast at lowest low water of spring tides is about 2.54 m. Mean sea level is for the neighbourhood of Den Helder 1.13 m higher (for Terschelling more than that), so that the mean water height would be 3.7 m or more. As the surface of the western part is about 1560 km^2 the volume at mean tide would be about 5.8 km^3 .

As the total populations of cockles and mussels pump at least some 0.041 km^3 a day they would pump a volume of water comparable to that of the western Waddensea in about 140 days or 2.6 times that volume in one year.¹ This does not mean, of course, that they would pump the whole water mass of the area 2.6 times a year, since they would pump part of the water again and again, and another part of it not at all. The result, however, would be all the same: that after not too long a period of time the water would have been largely deprived of its suspended organic matter, and how much material would be available to the animals would depend on the relation between the time necessary for its depletion and that necessary for the production of "new" organic material. In other words, the duration of the life-cycle of the organic matter would govern the whole as is the case in any closed body of water.

Now, it is difficult to believe that a population, which is so large that part of it may deprive its water mass from all food within 140 days, could do without a supply of food from outside. It may therefore be assumed that such a supply is necessary to maintain the population at such a high level. There is the more reason to suppose so, because there often may be a transport of organic material from the western Waddensea here studied to the east. The basin as a whole is very shallow and

¹ LINKE (1940) says that "allein auf der Wattfläche zwischen Juist und dem Festland, die etwa 150 qkm gross ist und bei Tidehochwasser einen Wasserinhalt von 250 Millionen cbm hat, von den dort lebenden Miesmuscheln täglich über 5 Millionen cbm Wasser durch Filtration restlos von Sinkstoffen befreit werden". It would mean that the mussels there would pump the whole watervolume in 50 instead of 140 days. This is not at all impossible, because so much depends on the quantities of mussels in relation to the watervolume. Moreover, our own estimation may be too low. LINKE does not mention the data, however, on which his calculations are based: one would like to know the average quantities of mussels present in the area in question as well as the average quantities of water supposed to be pumped per mussel of a certain size per day.

southwestern winds are dominant; transport may therefore easily take place and this must mean a constant loss. A second loss of organic material is caused by the fisheries. Whereas the quantities of cockles fished (for description see KREGER, 1939) are as a rule small, the quantities of mussels may be quite important and represent several millions of kilograms. A closed body of water without an import of food from outside could never continue producing such large numbers of animals for a series of years.

All this means that the second process mentioned above, that of the interchange between the Waddensea and the water surrounding it, must be very important.

A certain quantity of fresh water, on an average about 10^{10} m³ per year or 0.014 km³ per tide, is discharged into the Waddensea and mixes with the water of the Waddensea itself and with that entering every tide from the North Sea. According to measurements of the Rijkswaterstaat the latter quantity (entering through Marsdiep, Eyerlandse Gat and Vlie) is about 2 km³, so that at high tide, when the total volume of the Waddensea is about 6.8 km³, the latter are composed of 2 km³ of water from the North Sea, 0.014 km³ of fresh water and some 4.8 km³ of water of the Waddensea itself. The relation between the water entering from the North Sea and the fresh water is about 140:1, the North Sea water must therefore be of much more importance to the Waddensea than the fresh water. It must be realized, however, that part of the 2 km³ of water from the North Sea entering the Waddensea every tide left the latter during the foregoing ebb. Those 2 km³ do not, therefore, represent true North Sea water, but a mixture of water from the North Sea and the outer part of the Waddensea, in which the quantity of North Sea water increases outward and increases more and more as high tide is approached. The fact remains, however, that the influence of the North Sea water must be many times greater than that of the fresh water. Therefore, if it is the interchange between the Waddensea and its neighbouring waters, which makes food production possible on a large scale, the source for such food must in the very first place be found in the North Sea.¹

¹ LINKE (1940), whose paper I saw after my paper had been written, is apparently of opinion that the suspended matter present in the German Waddensea is chiefly formed within the latter. "Für die Emsmündung konnte nachgewiesen werden, dass Flusseinspülungen keine Rolle spielen. Unsicher ist hingegen noch der Einfluss von See her, besonders aus den grossen Schlickgebieten, die in der Nordsee vor den friesischen Küsten liegen. Damit ist für einen grossen Teil des Schlickes die Bildungsstätte bekannt, so dass die Frage der in einem bestimmten Zeitraum neu gebildeten Schlickmenge untersucht werden kann." As long as it is uncertain, however, whether the North Sea may not be an important source for the material in question, we should not suppose that the latter is chiefly formed within the Waddensea itself.

It is not at once clear how the North Sea water entering the Waddensea may cause such favourable conditions in the latter. One is inclined to believe that its *direct* influence must be small. Though 2 km^3 of mixed North Sea and Waddensea water enter the Waddensea every tide the combined populations of cockles and mussels according to our calculations do not pump more than 0.041 km^3 a day or only some 0.020 km^3 per tide. Even if this figure would be too low the quantity pumped can only be small compared with the quantity entering from the North Sea. Further, only part of the total mollusk population comes into direct contact with the "new" water, so that the quantities of North Sea water pumped must be quite low, even if the fact is taken into account that the feeding activity of such largely intertidal animals is greatest during the hours of high water, when the influence of the North Sea is maximal. The favourable influence of the water from the North Sea must therefore be largely an indirect one.

In the chapter Environment the opinion was expressed that the mixing of water masses of different character from the point of view of food production may be especially valuable, because organisms inhabiting these masses may be killed, together with detritus from that water may sink to the bottom and enrich the bottom water. I suppose this to be an important cause for the richness of coastal water generally. Within the Waddensea this material is transported inward and much larger quantities of food must thus become available to the mollusks than would be the case along the direct way alone. Food is here meant to include plankton from the North Sea, disintegrated plankton, detritus from the North Sea, detritus formed within the Waddensea from disintegrated North Sea plankton, and, finally, plankton organisms which grew up on the chemical compounds after mineralization of the organic material originating from the North Sea.

Summarizing, these suppositions come to the following.

The Waddensea, if it were a closed basin, could never produce such large amounts of animals as actually do exist and are fished there. It owes part of its organic matter, forming the base for its food supply, to the fresh water and especially to the water from the North Sea entering it. Part of this material will be used directly, but the greater part will gradually move inward and then become available to the animals indirectly. Through the simpleness of the sieving mechanism of the mollusks part of the organic material is refused, whereas part of it is excreted with the faecal pellets. The latter are not easily broken down, with the result that part of the organic material returns into the cycle only after a long lapse of time. A large quantity of it is thus accumulated. Another large part of the organic material brought in from the

North Sea will be stored in the flesh of the millions of animals. This part too returns into the cycle after a certain lapse of time, but this lapse must be much shorter than that of the faeces and this food is therefore earlier available again.

The above conclusion, however, that the Waddensea, if it were a closed basin, could never feed such large numbers of animals as actually do exist there, does not mean that the organic material of the Waddensea itself would not be important also. It goes without saying that both kinds of food sources cannot be separated and that they are used as one whole. It is further clear that within this whole the Waddensea-material itself cannot be neglected. If, namely, thanks to the favourable influence of the North Sea, a large population of animals is built up, in which great quantities of organic material are accumulated, the niveau of organic material within the Waddensea reaches a high level, so that a constant flow of organic material and a constant production of new material from it must be the result. Cockles and mussels themselves may be taken as an example. We came to the conclusion that their total within the Western Waddensea may amount to some 8000 million individuals. If one individual on the average would represent only 2000 mg (dry weight) of organic material their total represents at least some 16 million kg. If the average life cycle of these mollusks, as supposed above, would be about 3 years, 5 million kg of organic material at the very least would be furnished annually by cockles and mussels alone. Since, according to our earlier calculations (p. 227) the combined populations of cockles and mussels may pump some 40 million kg of organic material a year it is obvious that the quantities formed "by the Waddensea itself" must represent a considerable part of the whole, even if the fact is considered that much of the above 5 million kg is lost in the cycle. We can probably best say, therefore, that, though the high niveau of the organic material reached within the Waddensea is certainly due to the favourable influence of the North Sea, the latter does little more than regularly adding to the large amount of material already present, thus counteracting its losses.

VII. SUMMARY

The paper means an attempt to evaluate the rôle of bivalve mollusks, especially cockles and mussels, in matters of sedimentation in the western half of the Dutch Waddensea. It deals with the ecological needs of both species and their dependence on environmental factors, and also with the quantity and composition of the material suspended in the water and the source of its organic part, which is used for food.

It contains a concise summary of the feeding biology of bivalve mollusks and finally tries to evaluate the influence of the latter in matters of sedimentation.

1. The Waddensea is inhabited by a small number of species which can cope with (and possibly need) great differences in the quantity of light and suspended material, salinity and temperature, the strength of the currents and the changes in depths. But these animals have at their disposal extensive areas where competition with other species is less important than elsewhere and where food is abundant; they can therefore be numerous. Cockle and mussel should be seen in this light.

2. Cockles are restricted to a sandy bottom in shallow water. The larvae during or after metamorphosis presumably find the latter through their need of rather strong light. They can only settle where currents are weak. Since food conditions may be better where currents are stronger the places of easy settling need not be the best places for growth, with the result that the favourable areas for young and old animals are not always the same. Generally speaking, cockles are quite regularly distributed over the sands, their numbers changing rather gradually with the change of current velocities.

3. Mussels need a more or less firm substratum in shallow water. Their larvae too probably need a fair amount of light during the time of attachment. They settle especially on algae, from which, however, they loosen their hold after some time, to exchange them for another substratum. The byssus threads are quite valuable from this point of view, since they represent a semi-permanent form of attachment. After loosening their hold the young mussels have themselves carried through the currents. During this transport mussel banks catch them at haphazard. Mussel banks form the best substratum for settling since they contain so many niches. The congregation of thousands of mussels in mussel banks is not a result of social behaviour based on smell, but of the fact that there are no better niches for mussels than those between mussels. Mussel banks are especially lying along and over creeks. The reason is that not too weak and not too strong currents are optimal for them.

4. The matter suspended in the water of the Waddensea, averaging about 25 mg (dry weight) per litre, has about the following composition: sand about 44, shellsand 18, clay 8, Fe_2O_3 18, organic material 12 %. These figures are percentages of the dry total at 120° of all suspended material, plankton and organic detritus included. Especially the quantity of sand may show great differences from place to place and from one moment to the other. From the point of view of mollusk activity especially the 12 % of organic material are of interest.

5. The feeding biology of bivalves is dealt with in some detail in chapter IV under the following heads: 1. the number of hours the animals pump per day; 2. the quantities of water which are pumped; 3. the part of the suspended matter, which is pumped in; 4. the part of the material pumped in retained as food; 5. the way in which a separation between useful and unuseful takes place; 6. the part of the material retained which is rejected or accepted; 7. the part of the accepted material which is digested; 8. the quantity and composition of the faeces.

This chapter represents a review of the literature (with some new additions), which serves as a base for the calculations and conclusions following thereafter.

6. Chapter V deals with the activities of cockles and mussels within the Waddensea and with estimates about their rôle in sedimentation.

One cockle in the course of one year may be assumed to take in and fix at least some 44.000 mg (dry weight) of suspended matter (plankton included) and to reject at least some 17.000 mg of faeces. The remaining 27.000 mg are partly ejected as pseudofaeces, whereas the rest represents food. The number of cockles in the area dealt with is estimated at 6×10^9 individuals of 2 years old at the very least. They take in at least some 264 million kg (dry weight) of suspended matter a year and give off some 100 million kg of faeces. They further produce some 18–24 million kg of shells annually.

The mussel population of the area is estimated at about 70 million old, some 500 million halfgrown, and some 1500 million young mussels of about one year old, some 2000 million in all. This certainly is a very low estimate.

The quantity of suspended matter withdrawn from the water may be about one fourth that withdrawn by the combined cockles. The mussels produce 4–5 times less shell weight than the cockles.

Shells, faeces and pseudofaeces of cockles and mussels combined may at the very least represent some 250 million kg (dry weight) of material per year. This material is less easily carried away than before it had passed the animals, but in this connection there is much difference between the two species of bivalves dealt with.

It is difficult to say anything on the relation between the influence of cockles and mussels on sedimentation and sedimentation as a whole.

7. The source of the organic material, on which the millions of individuals inhabiting the Waddensea are built up, is found in the very first place in the North Sea. If the Waddensea were a closed basin it could never feed so many animals. At the same time, the quantity of organic material present in the water per unit of volume is smaller in the North Sea than in the Waddensea. It is accumulated in the

Waddensea through processes, of which mollusk activity represents one. Material from the North Sea is constantly laid down here. Nevertheless, the favourable influence of the North Sea on the Waddensea is certainly chiefly indirect, the North Sea doing little more than regularly adding to the large amount of material already present. For detailed argumentation the reader is referred to chapter VI.

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THE PREFERENCE OF SOME NUDIBRANCHS FOR CERTAIN COELENTERATES

by

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I. INTRODUCTION

In 1949 Miss STEHOUWER studied the behaviour of the nudibranchiate slug *Aeolidia papillosa* (L.), which normally feeds on the sea anemone *Metridium senile* (L.). She tried to find out whether it can locate its prey by scent, and, if so, whether, it is also attracted by other species of anemones. She observed that *Aeolidia* is more strongly attracted by *Metridium senile* than by some other species studied, but it remained an open question to her whether quality or quantity of scent causes this difference.

Hoping to get a somewhat broader base for further work in this direction the experiments were extended in two ways:

1. by studying the behaviour of *Aeolidia papillosa* in relation to some other species of Coelenterates;
2. by investigating the reaction of another nudibranch species in order to make a comparison between the latter and *Aeolidia papillosa* possible.

The work was carried out at the Zoological Station, Den Helder, between the middle of May and the middle of October, 1951. We are very grateful to Dr J. VERWEY, Director of the Station, for suggesting the subject and for his assistance in the drafting and translation of this paper; to Ir J. J. BEZEM, Zoological Laboratory of Utrecht University, and to Dr J. WESTENBERG, Zoological Station, Den Helder, for their assistance in statistical matters; to Mr A. C. H. VAN LIESHOUT, Commissioner of Pilotage at Den Helder, who gave us many facilities for obtaining animals from buoys; and, finally, to Mr C. SWENNEN, Den Helder, whose knowledge of nudibranchs and constant help in obtaining material were unsurpassed.

II. MATERIAL AND METHODS

Unpublished observations by SWENNEN show that some 25 species of nudibranchs have been found near Den Helder. There seemed ample opportunity, therefore, to extend the work already started to more

species. With such experiments, however, in which large numbers of specimens are needed, it is very difficult to find sufficient material of any one species over a period of several months. Most of the species are found only occasionally, several of them may be very common in certain years, but altogether wanting in others, some species are less suitable because of their small size or because they are difficult to keep. We tried to work with *Tergipes despectus* (Johnston), which was common in early summer, but it is so small that too much time is needed to clear the hydroids (used in the experiments) of their slugs and this constitutes a great drawback.

After some failures the work was restricted to *Aeolidia papillosa* (L.) and *Cratena aurantia* (A. & H.), whereas a few observations were made on *Dendronotus frondosus* (Ascanius), which, however, needed lower temperatures than we could offer.

Aeolidia papillosa was collected in the immediate neighbourhood of the coast near Den Helder. *Cratena aurantia* was collected from hydroids dredged in the Nieuwediep, later on from buoys, regularly controlled by an inspection vessel of the Hydrographic Service. These furnished us with abundant material of nudibranchs.

The hydroids and anemones used were collected in the Nieuwediep (especially on mooring-rafts) and along the shore, later on especially from buoys. Inevitably the hydroids were always slightly damaged in collecting. Moreover, in our experiments, *Tubularia* always lost its hydranths; as far as we could make out this did not influence the results; under natural conditions *Cratena aurantia* was always found on its hydrocaulus, mostly on the base of the latter.

The method used in testing the slugs was in principle the same as that used by Miss STEHOUSER, and for a good understanding her description should be consulted. Sea water from the circulation system of the Station flowed via an aquarium with constant level into two small aquaria, one containing a certain Coelenterate species, the other serving as a check. The water from both aquaria was conducted through plastic (polyvinylchlorid) siphons with an inner diameter of 15 mm to a third aquarium containing slugs. The slugs, if attracted, would pass the siphons and accumulate in the Coelenterate aquarium. To this end, current velocities in the siphons had to be small. Miss STEHOUSER in her experiments placed the siphons close together. We placed them at opposite sides of the aquarium in the assumption that there might be a better concentration gradient then, which would make it easier for the slugs to find the right siphon. No observations were made to test this assumption, however.

The number of slugs used in any one experiment depended on the number of specimens available at that moment and on other factors.

If possible, enough experiments were carried out so that the results left no doubt as to the validity of the answer.

Each experiment lasted 24 hours, after which period the number of slugs in each of the three aquaria was counted. The numbers are given in the tables. From them the totals for a whole series of experiments have been counted. It should be realized, however, that most animals were used several times in succession. The totals therefore refer to total numbers of single observations, and not to totals of animals.

The degree of attraction, exercised by a certain Coelenterate species, is given by the relation between the number of slugs found with the Coelenterate and the total number of slugs used. This percentage is compared with that of slugs found in the control aquarium. Thus we can say that *Cratena aurantia* is strongly attracted by *Tubularia indivisa*, since more than 80 % of all animals tested reached the hydroid, whereas only 1 % reached the control aquarium.

When these same percentages are used, however, to compare the attractive force of different Coelenterate species a difficulty arises. The value of the percentages depends on the number of active slugs. The inactivity of slugs, however, may be due to two causes:

1. to the fact that for some reason they are quite unresponsive;
2. to the absence of the adequate stimulus which evokes a reaction.

In all cases, therefore, in which slugs were not attracted by a certain Coelenterate species, a control experiment had to be carried out with another species, the preference of which had been shown to exist in former experiments, in order to see whether the slugs did take the latter. In all such cases the result was positive, so that we may be sure that negative results were never due to true inactivity of the animals in question, but to inadequateness of the stimulus.

This being the case, we are more or less allowed to use the percentages obtained for a comparison of the different Coelenterate species. If 60 % of *Cratena* is found to be attracted by *Tubularia larynx* and 80 % by *Tubularia indivisa* and these percentages are the same in different series of experiments we are inclined to attach much value to this difference. It should always be remembered, however, that inactivity as such may change from moment to moment and that the figures can never be considered absolute.

It should be added that in our first experiments the slugs received no food during the 24 hours prior to the experiments. It was found, however, that the same results were obtained when the animals did get food during this period. In our later experiments, therefore, food was no longer withheld.

A similar method as that used by Miss STEHOUWER and us was used by D. DAVENPORT (1950), who studied the attraction exercised by certain echinoderms

on their polychaete commensals of the genus *Arctonoe*. Davenport, however, kept his echinoderms (to be compared with our anemones) for some time in stagnant seawater. He then transferred the water with echinoderms to the aquarium of his test-apparatus. This was done in the hope that the scent might accumulate in the water to be tested. This forms an unnecessary complication: the waterlevel in the aquaria went down during the experiments, the current velocities changed and the experiments could not be continued for longer periods. Davenport, moreover, let his animals choose in a rather narrow forked glass tube, in which both kinds of water (with and without scent) mixed, with the result that part of his animals were easily led astray. It is certainly much better to give the animals an aquarium in which both kinds of water mix, so that there is a concentration gradient like we gave to *Aeolis*. Davenport's method has apparently been developed on the assumption that an accumulation of scent emitting substance would be required for a definite attraction. Our experiments, however, appear to refute this view.

III. EXPERIMENTS

I. AEOLIDIA PAPILLOSA (L.)

Miss STEHOUWER tested the behaviour of this species in relation to *Metridium senile* (L.), *Diadumene cincta* (Stephenson), *Actinothoe anguicoma* (Price) [possibly mixed with *Sagartia troglodytes* (Price)], and *Tealia felina* (L.). These experiments were extended by us by testing the following species:

A. Actiniaria: *Metridium senile* (L.), *Actinia equina* L.

B. Hydroidea: *Tubularia indivisa* L., *T. larynx* Ell. & Sol., *Laomedea flexuosa* Alder, *L. longissima* (Pall.), and *Hydractinia echinata* (Flem.).

The reactions of *Aeolidia papillosa* to *Metridium senile* have been studied by Miss STEHOUWER, so that there was little need to study them

TABLE I

Behaviour of *Aeolidia papillosa* in relation to *Metridium senile*. Control on the negative behaviour of *Aeolidea* in relation to *Laomedea flexuosa* (see table VIII). The 3 rows of figures denote numbers of *Aeolidia*.

Number of experiment	Date (September)	<i>Metridium senile</i>	Control	No reaction
1	22	6	0	19
2	22	17	0	8
3	22	9	0	15
4	23	13	0	12
5	23	12	0	12
6	24	11	0	14
7	25	12	0	12
8	25	11	0	13
9	25	4	0	21
Total		95	0	126
Percentage . . .		43.0	0	

again. To be certain, however, of the value of negative results, those animals, which had failed to show a reaction to some species of hydroids, were afterwards confronted with *Metridium senile*. In this way data on the slug's behaviour in relation to *Metridium senile* were obtained, which corroborate Miss STEHOUEW's results.

A. Actiniaria

1. *Metridium senile* (L.). 3 series of 9-10 experiments each were carried out with *Metridium senile* of about 2-3 cm diameter. These three series at the same time served as checks on the results obtained for *Laomedea flexuosa*, *L. longissima*, and *Tubularia larynx*. For results see tables I-III.

TABLE II

Aeolidia papillosa in relation to *Metridium senile*. Control on the negative behaviour of *Aeolidia* in relation to *Laomedea longissima* (table IX). The 3 rows of figures denote numbers of *Aeolidia*.

Number of experiment	Date (September)	<i>Metridium senile</i>	Control	No reaction
1	26	12	0	12
2	26	15	1	8
3	26	14	0	11
4	27	13	0	11
5	27	14	1	19
6	28	7	0	18
7	29	4	0	20
8	29	5	0	19
9	29	8	0	11
Total		92	2	129
Percentage . .		41.3	0.9	

TABLE III

Aeolidia papillosa in relation to *Metridium senile*. Control on the negative behaviour of *Aeolidia* in relation to *Tubularia larynx* (table VII). The 3 rows of figures denote numbers of *Aeolidia*.

Number of experiment	Date (September)	<i>Metridium senile</i>	Control	No reaction
1	11	10	0	8
2	13	3	1	21
3	15	3	2	20
4	16	6	1	18
5	18	9	0	14
6	18	7	0	17
7	20	7	0	16
8	20	12	0	10
9	21	10	0	15
10	21	9	0	15
Total		76	4	154
Percentage . .		32.5	1.7	

The result of these 3 series is that in 28 experiments with a total of 678 observations, 43.0, 41.3 and 32.5 % of the animals were attracted to *Metridium* and 0, 0.9 and 1.7 % to the aquarium without anemones. The average percentages are 39.0 and 0.9 respectively. The figure 39.0 % is lower than the 52 % found by Miss STEHOUWER, but we need not expect the same values in experiments in which so much may depend on the activity or sluggishness of the animals. In Miss STEHOUWER's series, moreover, damaged anemones may have been included, which would make much difference (see below).

2. *Actinia equina* L. With this species one series of 12 experiments was made, the results of which are shown in table IV.

TABLE IV
Aeolidia papillosa in relation to *Actinia equina*.

Number of experiment	Date (Sept.—Oct.)	<i>Actinia equina</i>	Control	No reaction
1	29	17	1	6
2	29	8	0	15
3	29	15	0	4
4	30	23	0	5
5	30	8	0	11
6	30	1	0	19
7	1	10	0	14
8	1	8	1	10
9	1	9	1	10
10	2	20	2	5
11	2	6	0	11
12	2	8	1	11
Total		133	6	121
Percentage . . .		51.2	2.3	

It is clear that *Actinia equina* attracts *Aeolidia* rather strongly. The percentage of slugs found with the anemone is not exact, however, because of the presence of damaged anemones. During the experiments the slugs started feeding on some of the *Actinia* and the wounded anemones caused an extra-attraction of slugs. The same was the case in Miss STEHOUWER's experiments with *Aeolidia papillosa* and *Metridium senile*. To prove this influence the results for undamaged and damaged *Actinia* are given separately below.

Table V shows that it makes much difference whether *Actinia equina* is damaged or not, a point which is treated in more detail in the addendum to this paper. It is therefore certain that the percentage of 51.2 found in table IV cannot be compared with the average percentage found for *Aeolidia* and *Metridium senile*, which amounted to 39. The latter

percentage can best be compared with the percentage of 38.5 found for undamaged *Actinia equina* in table V.

Furthermore, when slugs start feeding on anemones it is possible that a stronger attraction is supplied to the other slugs and in this inconspicuous way the results of the experiments may be influenced.¹

Anyhow, the experiments show that *Actinia equina* attracts *Aeolidia papillosa* rather strongly and that there is apparently much agreement between the attractiveness of *Actinia* and *Metridium*.

TABLE V
Aeolidia papillosa in relation to undamaged and damaged *Actinia equina*.

		<i>Aeolidia</i> -numbers					Total	Percentage
2 <i>Actinia</i> , undamaged	<i>Actinia</i>	8	8	8	6		30	38.5
	Control	0	0	1	0		1	1.3
	No reaction	15	11	10	11		47	
2 <i>Actinia</i> , one undamaged, one damaged	<i>Actinia</i>	17	15	9	8	1	50	48.5
	Control	1	0	1	1	0	3	2.9
	No reaction	6	4	10	11	19	50	
2 <i>Actinia</i> , both damaged	<i>Actinia</i>	23	10	20			53	67.1
	Control	0	0	2			2	2.5
	No reaction	5	14	5			24	

B. Hydroidea

1. *Tubularia indivisa* L. A series of 9 experiments was carried out with *Tubularia indivisa*. Its results are given in table VI.

TABLE VI
Aeolidia papillosa in relation to *Tubularia indivisa*.

Number of experiment	Date (October)	<i>Tubularia indivisa</i>	Control	No reaction
1	7	1	4	21
2	7	4	0	22
3	7	2	1	11
4	8	2	3	27
5	8	3	3	14
6	8	0	0	12
7	9	2	3	23
8	9	2	2	15
9	9	1	0	10
Total		17	16	155
Percentage . . .		9.0	8.5	

¹ Therefore, the method was somewhat changed in later experiments, so that the slugs could no longer feed on the anemones.

Since comparable numbers of slugs are found in both the Coelenterate and the control aquarium the experiments do not prove that *Aeolidia* is attracted by *Tubularia indivisa*. The rather high number of slugs found in the control aquarium is a strange fact, to which we return below.

2. *Tubularia larynx* Ell. & Sol. A series of 10 experiments was made with *Tubularia larynx*. The results are given in table VII.

TABLE VII
Aeolidia papillosa in relation to *Tubularia larynx*.

Number of experiment	Date (September)	<i>Tubularia larynx</i>	Control	No reaction
1	10	1	3	6
2	12	1	1	15
3	14	1	2	22
4	15	2	1	22
5	17	0	0	25
6	17	1	0	24
7	19	1	0	22
8	19	0	0	22
9	20	0	1	20
10	20	0	1	19
Total		7	9	197
Percentage . . .		3.3	4.2	

The slugs used in this experiment were afterwards tested with *Metridium senile*; 32.5 % of them reacted positively on that species (see table III). It is clear, therefore, that the low percentage in the case of *Tubularia larynx* must be due to the fact that *Aeolidia* is not attracted by this hydroid.

3. *Laomedea flexuosa* Alder. 9 experiments were made to test the reaction of *Aeolidia* to *Laomedea flexuosa*, a species which is rather common in the Nieuwediep. The results are given in table VIII.

The slugs were afterwards tested with *Metridium senile* (compare table I). Since 43.0 % of them reacted positively on that species, the negative result with *Laomedea* is beyond doubt. In view of this fact it is interesting that the value for the hydroid is even lower than that for the control aquarium, a point to which we shall refer below (p. 251).

4. *Laomedea longissima* (Pall.). A series of 9 experiments was carried out with this species, compare table IX.

The slugs were afterwards tested with *Metridium senile* (see table II).

As 41.3 % of them reacted positively on that species it is clear that *Laomedea longissima* does not attract *Aeolidia*. Here also it is striking that the control aquarium attracts more slugs than the hydroid.

TABLE VIII
Aeolidia papillosa in relation to *Laomedea flexuosa*.

Number of experiment	Date (September)	<i>Laomedea flexuosa</i>	Control	No reaction
1	21	0	0	25
2	21	0	1	24
3	21	1	2	21
4	22	0	3	22
5	22	2	1	21
6	23	0	1	24
7	24	0	3	21
8	24	1	1	22
9	24	0	0	25
Total		4	12	205
Percentage . . .		1.8	5.4	

TABLE IX
Aeolidia papillosa in relation to *Laomedea longissima*.

Number of experiment	Date (September)	<i>Laomedea longissima</i>	Control	No reaction
1	25	1	2	22
2	25	0	1	23
3	25	0	1	24
4	26	0	1	23
5	26	2	1	21
6	27	0	2	23
7	28	1	0	23
8	28	0	2	22
9	28	1	0	18
Total		5	10	199
Percentage . . .		2.3	4.7	

5. *Hydractinia echinata* (Flem.). Near Den Helder this hydroid is especially found on Gastropod shells inhabited by the hermit crab (*Eupagurus bernhardus*). *Aeolidia papillosa* will, therefore, rarely get an opportunity to feed on it. A series of 9 experiments was carried out with it (table X). The result is negative and it is therefore to be regretted that a control experiment with *Metridium senile* was omitted in this case. In view of the positive result of all the other control experiments made, however, we assume that *Aeolidia* is not attracted by this hydroid.

It is interesting to find that here again the value for the control aquarium is somewhat higher than that for the hydroid.

TABLE X

Aeolidia papillosa in relation to *Hydractinia echinata*.

Number of experiment	Date (October)	<i>Hydractinia echinata</i>	Control	No reaction
1	3	0	0	24
2	3	0	0	21
3	3	0	5	18
4	4	0	2	26
5	4	2	2	19
6	4	1	1	20
7	5	3	1	26
8	5	1	1	22
9	5	1	0	15
Total		8	12	191
Percentage . . .		3.8	5.7	

Summarizing the results for the behaviour of *Aeolidia papillosa* in relation to the hydroids tested we see that the numbers of slugs are not greater in the hydroid than in the control aquarium. It is rather the contrary that occurs. Most of the percentages for the control aquaria are somewhat higher than those for the aquaria with hydroids and the impression is gained that the hydroids may have repelled the slugs more or less. This might especially hold good for the *Laomedea* species. Our hope that statistical treatment might give certainty in this respect proved idle, however, as follows from the contents of the addendum at the end of this paper.

There cannot be the least doubt that *Aeolidia papillosa* is attracted more strongly by sea anemones (especially *Metridium* and *Actinia*) than by hydroids.

2. CRATENA AURANTIA (A. & H.)

Cratena aurantia is a rather small nudibranchiate slug (about 10–12 mm long), which lives on *Tubularia*. The behaviour of this species in relation to the following Coelenterate species was tested:

- A. Actiniaria: *Metridium senile* (L.), *Diadumene cincta* (Stephenson), *Actinothoe anguicoma* (Price), *Sagartia troglodytes* (Price), *Actinia equina* L.
 B. Hydroidea: *Tubularia indivisa* L., *T. larynx* Ell. & Sol., *Laomedea flexuosa* Alder, *L. longissima* (Pall.), and *Hydractinia echinata* (Flem.).

A. Actiniaria

1. *Metridium senile* (L.). One series of 3 experiments was carried out with *Metridium*, the results of which are given in table XI.

TABLE XI

Behaviour of *Cratena aurantia* in relation to *Metridium senile*.

Number of experiment	Date (July-August)	<i>Metridium senile</i>	Control	No reaction
1	21	0	0	50
2	5	0	0	50
3	7	0	0	24
Total		0	0	124
Percentage . .		0	0	

To exclude the possibility that *Cratena* would have shown no reaction because it was not in good condition, the same animals were tested with *Tubularia larynx*, on which species 53.3 % of the animals reacted positively (compare table XXII).

2. *Diadumene cincta* (Stephenson). One series of 3 experiments was carried out with *Diadumene*, see table XII.

TABLE XII

Behaviour of *Cratena* in relation to *Diadumene*.

Number of experiment	Date (July-August)	<i>Diadumene cincta</i>	Control	No reaction
1	31	0	0	50
2	5	0	0	50
3	7	0	0	24
Total		0	0	124
Percentage . .		0	0	

These experiments were not followed by a control experiment with *Tubularia*.

TABLE XIII

Behaviour of *Cratena* in relation to *Actinothoe*.

Number of experiment	Date (Aug.-Sept.)	<i>Actinothoe anguicoma</i>	Control	No reaction
1	13	0	0	25
2	16	1	0	39
3	18	0	0	25
4	1	0	0	30
5	1	0	0	25
6	2	0	0	37
Total		1	0	181
Percentage . .		0.5	0	

3. *Actinothoe anguicoma* (Price). One series of 6 experiments was carried out with *Actinothoe*. The results are given in table XIII.

The experiments were followed by a control experiment with *Tubularia larynx*, which gave positive behaviour in 61.8% of the animals tested (table XXIII).

4. *Sagartia troglodytes* (Price). One series of 4 experiments was carried out with *Sagartia troglodytes*. The results are shown in table XIV.

TABLE XIV
Behaviour of *Cratena* in relation to *Sagartia troglodytes*.

Number of experiment	Date (September)	<i>Sagartia troglodytes</i>	Control	No reaction
1	5	0	0	33
2	11	0	0	25
3	13	0	0	20
4	15	0	0	34
Total		0	0	112
Percentage . . .		0	0	

After that, a control experiment with *Tubularia indivisa* was made. This gave positive behaviour in about 80% of the animals tested (compare table XVII).

5. *Actinia equina* L. A series of 8 experiments was carried out with *Actinia equina*, one of the two species which gave fine positive results with *Aeolidia papillosa*. With *Cratena* the result was entirely negative, see table XV.

TABLE XV
Behaviour of *Cratena* in relation to *Actinia equina*.

Number of experiment	Date (Sept.-Oct.)	<i>Actinia equina</i>	Control	No reaction
1	18	0	0	25
2	18	0	0	12
3	19	0	0	25
4	19	0	0	25
5	19	0	1	11
6	21	0	0	23
7	8	0	0	25
8	9	0	0	25
Total		0	1	171
Percentage . . .		0	0.6	

After this result had been obtained, a control experiment with *Tubularia indivisa* was made, which gave positive behaviour in about 78% of the animals tested (table XVIII).

B. *Hydroidea*

1. *Tubularia indivisa* L. A series of 9 experiments was carried out with *Tubularia indivisa*. The latter species, moreover, was tested to check the negative results obtained for *Sagartia troglodytes*, *Actinia equina*, *Laomedea flexuosa*, and *Hydractinia echinata*. In this way results for 5 series, comprising 24 experiments and dealing with a total of 689 observations, have been obtained. The results are given in tables XVI–XX.

TABLE XVI
Behaviour of *Cratena* in relation to *Tubularia indivisa*.

Number of experiment	Date (August)	<i>Tubularia indivisa</i>	Control	No reaction
1	20	29	1	8
2	20	30	0	6
3	21	27	0	6
4	21	25	0	4
5	22	35	0	3
6	24	34	0	3
7	25	25	0	6
8	27	23	2	3
9	28	17	0	2
Total		245	3	41
Percentage . . .		84.8	1.0	

TABLE XVII

Behaviour of *Cratena* in relation to *Tubularia indivisa*. Control on the negative behaviour of *Cratena* in relation to *Sagartia troglodytes* (see table XIV).

Number of experiment	Date (September)	<i>Tubularia indivisa</i>	Control	No reaction
1	6	24	1	6
2	12	20	1	3
3	14	17	0	2
Total		61	2	11
Percentage . . .		82.4	2.7	

In the experiments mentioned in table XIX the *Tubularia indivisa* used was in very bad condition. We therefore believe this may have been the cause of the rather low percentage of attraction.

It follows from tables XVI–XX that *Cratena* is attracted by *Tubularia indivisa* in about 84, 80, 78, 61.5 and 82.5 % of the total number of animals tested in each of the five series. Altogether, 689 observations have been made, of which 564 were positive, whereas the controls gave a total of 9. This means that *Cratena* was found with *Tubularia*

TABLE XVIII

Behaviour of *Cratena* in relation to *Tubularia indivisa*. Control on the negative behaviour of *Cratena* in relation to *Actinia equina* (see table XV).

Number of experiment	Date (September)	<i>Tubularia indivisa</i>	Control	No reaction
1	19	21	0	4
2	19	11	0	1
3	20	18	0	3
4	20	17	0	3
5	20	5	1	4
6	22	13	0	7
Total		85	1	22
Percentage . . .		78.7	0.9	

TABLE XIX

Behaviour of *Cratena* in relation to *Tubularia indivisa*. Control on the negative behaviour of *Cratena* in relation to *Laomedea flexuosa* (see table XXIV).

Number of experiment	Date (September)	<i>Tubularia indivisa</i>	Control	No reaction
1	21	12	0	3
2	23	6	0	2
3	25	7	0	7
4	27	5	1	4
Total		30	1	16
Percentage . . .		63.8	2.1	

TABLE XX

Behaviour of *Cratena* in relation to *Tubularia indivisa*. Control on the negative behaviour of *Cratena* in relation to *Hydractinia echinata* (see table XXVI).

Number of experiment	Date (September)	<i>Tubularia indivisa</i>	Control	No reaction
1	3	29	1	6
2	6	33	0	5
3	11	30	0	4
4	14	31	1	7
5	15	20	0	4
Total		143	2	26
Percentage . . .		83.6	1.2	

indivisa in 81.9%, whereas it was found in the control aquarium in only 1.3% of the single observations. More than 80% of the total, therefore, reacted positively to the hydroid. If the results given in table XIX are omitted because of the bad condition of the *Tubularia* used, the latter percentage amounts to 82.

2. *Tubularia larynx* Ell. & Sol. A series of 18 experiments was carried out with *Tubularia larynx*. Moreover, this species was used to control the negative results obtained with *Metridium senile* and *Actinothoe anguicoma*. In this way 25 experiments dealing with 535 observations were made. The results are given in tables XXI-XXIII.

TABLE XXI
Behaviour of *Cratena* in relation to *Tubularia larynx*.

Number of experiment	Date (June-July-August)	<i>Tubularia larynx</i>	Control	No reaction
1	30	3	0	9
2	30	2	0	13
3	30	7	1	7
4	1	10	0	5
5	1	8	0	7
6	3	12	0	3
7	3	12	0	3
8	5	5	0	10
9	5	1	0	14
10	8	6	0	3
11	8	9	0	5
12	12	11	0	4
13	12	10	0	5
14	26	4	0	6
15	26	6	0	4
16	27	24	0	14
17	27	24	3	13
18	12	16	0	9
Total		170	4	134
Percentage . . .		55.2	1.3	

TABLE XXII

Behaviour of *Cratena* in relation to *Tubularia larynx*. Control on the negative behaviour of *Cratena* in relation to *Metridium senile* (see table XI).

Number of experiment	Date (August)	<i>Tubularia larynx</i>	Control	No reaction
1	1	24	1	23
2	6	25	0	24
3	8	15	1	7
Total		64	2	54
Percentage . . .		53.3	1.7	

These experiments show that in the 3 series studied *Tubularia larynx* attracted 55.2, 53.3 and 61.7% of the animals tested, whereas the water without *Tubularia* got 1.3, 1.7 and 0.9%. Altogether, 535 observations have been made and these gave 300 times *Tubularia larynx*

TABLE XXIII

Behaviour of *Cratena* in relation to *Tubularia larynx*. Control on the negative behaviour of *Cratena* in relation to *Actinothoe anguicomma* (see table XIII).

Number of experiment	Date (August-September)	<i>Tubularia larynx</i>	Control	No reaction
1	14	18	0	7
2	17	16	0	14
3	19	12	0	9
4	3	20	1	10
Total		66	1	40
Percentage . . .		61.7	0.9	

against 7 times the control aquarium without *Tubularia*, i.e., 56.1 against 1.3 %. Apparently, there is a distinct preference for *Tubularia indivisa* compared with *T. larynx*, *T. indivisa* yielding a percentage of more than 80, *T. larynx* one of about 55 %. This point is statistically treated in the addendum to this paper.

3. *Laomedea flexuosa* Alder. This species was tested in one series of 8 experiments, the results of which are given in table XXIV.

TABLE XXIV

Behaviour of *Cratena* in relation to *Laomedea flexuosa*.

Number of experiment	Date (August and Oct.)	<i>Laomedea flexuosa</i>	Control	No reaction
1	15	0	0	16
2	20	0	0	21
3	22	0	0	10
4	24	0	0	16
5	26	0	1	11
6	4	0	0	35
7	5	0	0	46
8	7	0	0	25
Total		0	1	180
Percentage . . .		0	0.6	

A control experiment was made with *Tubularia indivisa*. This gave a positive reaction for 63.8 % of the animals (compare table XIX). It is therefore certain that *Cratena* is not attracted by *Laomedea flexuosa*.

4. *Laomedea longissima* (Pall.). A series of 11 experiments was carried out with *Laomedea longissima*. The results are given in table XXV.

The results create the impression that now and again *Cratena* reacts positively to *Laomedea longissima*. We believe, however, that the partly

TABLE XXV

Behaviour of *Cratena* in relation to *Laomedea longissima*.

Number of experiment	Date (July)	<i>Tubularia larynx</i>	Control	No reaction
1	11	0	0	15
2	11	0	0	15
3	14	0	1	8
4	14	4	0	6
5	14	0	0	10
6	14	2	0	8
7	16	6	0	9
8	16	0	0	15
9	16	5	0	10
10	18	0	0	10
11	18	1	0	9
12	23	1	0	14
13	28	0	0	39
14	29	1	2	47
15	30	1	2	54
Total		21	5	269
Percentage . . .		7.1	1.7	

positive results may be due to the presence of fragments of *Tubularia larynx* in the *Laomedea* colonies. When these experiments were carried out, *Tubularia larynx* began to replace *Laomedea longissima* on the rafts. Quite small specimens of *Tubularia larynx* then regularly occurred within the colonies of *Laomedea*, and though we did our best to remove them fragments may have been overlooked. This possibility is excluded in the case of *Laomedea flexuosa*, since the latter was collected in places emerging at low tide, where *Tubularia larynx* does not occur.

5. *Hydractinia echinata* (Flem.). A series of 6 experiments was made with *Hydractinia echinata*. Its results are given in the next table.

TABLE XXVI

Behaviour of *Cratena* in relation to *Hydractinia echinata*.

Number of experiment	Date (September)	<i>Hydractinia echinata</i>	Control	No reaction
1	2	0	1	37
2	4	2	1	37
3	5	1	1	37
4	10	0	0	35
5	13	0	0	39
6	14	1	0	25
Total		4	3	210
Percentage . . .		1.8	1.4	

A control experiment was made with *Tubularia indivisa*, which attracted 83.6 % of the *Cratena*, whereas the control attracted 1.2 % (compare table XX). It is clear, therefore, that the slug is not attracted by *Hydractinia echinata*.

3. DENDRONOTUS FRONDOSUS (ASCANIUS)

The third species of nudibranchiate we worked with was *Dendronotus frondosus*, a northern form, which did not thrive in our aquaria. Moreover, it is rather uncommon near Den Helder, so that only very few experiments could be made. These were concerned with *Tubularia larynx* and not too much value should be attached to them, since the slugs were not very active.

TABLE XXVII
Behaviour of *Dendronotus* in relation to *Tubularia larynx*.

Number of experiment	Date (Juni-July)	<i>Tubularia larynx</i>	Control	No reaction
1	30	4	0	5
2	2	5	0	5
3	2	6	0	4
4	4	1	0	11
5	4	0	0	11
6	8	0	0	11
7	8	1	0	10
8	10	2	0	10
9	10	3	0	9
10	12	0	0	12
11	12	1	0	11
12	13	0	0	12
13	13	0	0	12
14	16	8	1	4
Total		31	1	127
Percentage . . .		19.5	0.6	

These experiments only show that *Dendronotus* is attracted by *Tubularia larynx*.

IV. GENERAL CONCLUSIONS

The results obtained for *Aeolidia papillosa* and *Cratena aurantia* are summarized in table XXVIII. The figures denoted with an asterisk have been taken from Miss STEHOUWER's publication.

This comparison shows that *Aeolidia papillosa* is chiefly attracted by *Metridium senile* and *Actinia equina*, whereas *Cratena aurantia* is attracted

TABLE XXVIII

Behaviour of *Aeolidia* and *Cratena* in relation to all species of Coelenterates investigated.

	<i>Aeolidia</i>		<i>Cratena</i>	
	Coelenterate	Control	Coelenterate	Control
<i>Metridium</i>	39	0.9	0	0
<i>Diadumene</i>	14 ¹	1 ¹	0	0
<i>Actinothoe</i>	9 ¹	0 ¹	0.6	0
<i>Sag. troglodytes</i>	—	—	0	0
<i>Tealia</i>	8 ¹	1-2 ¹	—	—
<i>Actin. equina</i>	38.4	1.2	0	0.6
<i>Tub. indivisa</i>	9.—	8.5	81.9	1.3
<i>Tub. larynx</i>	3.3	4.1	56.1	1.3
<i>Laom. flexuosa</i>	1.8	5.4	0	0.6
<i>Laom. longissima</i>	2.3	4.6	7.1	1.7
<i>Hydract. echinata</i>	3.7	5.6	1.8	1.4

¹ SWENNEN found indications that *Aeolidia papillosa* shows a different preference for *Actinothoe unguicoma* and *Sagartia troglodytes*. Since specimens of the latter species may have been among the *Actinothoe* used by Miss STEHOUEW her results obtained with *Actinothoe* should be considered with caution. — In our own experiments we took care to separate the two species well.

by *Tubularia indivisa* and *T. larynx*. Miss STEHOUEW, finding that damaged anemones attract more *Aeolidia* than undamaged ones, wondered whether quality or quantity of scent would play a part. Our data, obtained from two species of slugs studied under analogous conditions, show that quality of scent is apparently quite important. We may assume that only in this way can the fact be explained that *Metridium* attracted 39% of the *Aeolidia* studied and none of the *Cratena*. It follows from Miss STEHOUEW's data on *Metridium senile* and ours on *Actinia equina*, however, that quantity of scent is also important.

Further, the results for *Aeolidia papillosa* are interesting for two reasons. We may expect that the nudibranchs innately react on the scent of those Coelenterate species which represent their normal food and that species on which they do not feed are not incorporated in their reaction mechanism. One would therefore expect that there are attractive and non-attractive scents. Miss STEHOUEW has found, however, that some anemone species attract *Aeolidia* more strongly than others and that there is apparently such a thing as a gradation in attractive force. Further, our own figures show that some hydroids may even repel *Aeolidia*.

Gradation in attraction also comes to the fore in the results for *Cratena aurantia*. To this species, *Tubularia* is probably the only hydroid genus of importance, but of the two species studied *T. indivisa* attracts *Cratena* more strongly than does *T. larynx*. There must, therefore, be a gradation in the adequateness of the stimulus. In this connection it would be interesting to find out what chemical compound may be

made use of in the inborn reaction mechanism of the slug. A similar question has been worked out by Miss WREDE (1927) for the relation between *Glossosiphonia* and the snail *Physa*.

As to the second point, *Cratena aurantia* is apparently not repelled by any of the hydroids tested; the control aquaria always yield very low figures. Assuming that hydroids do repel *Aeolidia* the results would show that *Aeolidia* is attracted by some species of anemones and repelled by some species of hydroids, whereas *Cratena* is attracted by some species of hydroids and not repelled by other Coelenterate species. Attraction of one and repelling of another slug species would therefore not necessarily be caused by the same compounds.

For statistical treatment of some of the data the reader is referred to the addendum.

V. SUMMARY

The paper deals with the reaction of some species of nudibranchiate slugs to the scent given off by different species of sea anemones and hydroids.

Aeolidia papillosa is strongly attracted by two species of anemones (out of 5 species studied) and possibly repelled (at least not attracted) by 5 species of hydroids, whereas *Cratena aurantia* is attracted by 2 species of hydroids and not by the other 3 hydroid and the 5 anemone species studied.

The results of all experiments are summarized in table XXVIII. The species innately react to the scent of those Coelenterate species, which represent their normal food, and species on which they do not feed are not incorporated in their reaction mechanism. There are attractive and non-attractive scents. It was found, however, that *Aeolidia papillosa* is also more or less attracted by the 3 anemone species on which it feeds more or less exceptionally, and that *Cratena aurantia*, which feeds on 2 *Tubularia* species, is attracted more strongly by one of these than by the other. Apparently, there are different degrees of attraction and in this connection it would be important to study the scent emitting substance of the Coelenterate species used.

VI. LITERATURE

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VII. ADDENDUM

In order to test the reliability of the results statistical treatment was applied to some of the data.¹

First, we have applied the chi-squared test for independence of two variables in a 3×2 contingency table to the data given in table V (p. 248) concerning the attraction of *Aeolidia papillosa* (L.) by a set of *Actinia equina* L., of which none, one or two anemones were wounded respectively. The computation was carried out according to the following scheme:

$f_{1,1}$	$f_{1,2}$	$f_{1,3}$	
$w_{1,1} = \frac{Aa}{N}$	$w_{1,2} = \frac{Ba}{N}$	$w_{1,3} = \frac{Ca}{N}$	a
$t_{1,1}$	$t_{1,2}$	$t_{1,3}$	
$f_{2,1}$	$f_{2,2}$	$f_{2,3}$	
$w_{2,1} = \frac{Ab}{N}$	$w_{2,2} = \frac{Bb}{N}$	$w_{2,3} = \frac{Cb}{N}$	b
$t_{2,1}$	$t_{2,2}$	$t_{2,3}$	
A	B	C	N

In this scheme N represents the total number of observations; a, b, A, B and C are the marginal frequencies; $f_{i,j}$ is the observed frequency in each class; $w_{i,j}$ is the expected class-frequency calculated from the marginal frequencies on the assumption that the number of damaged anemones in each set has no effect on the attraction of *Aeolidia*; $t_{i,j}$

is defined by $\frac{(f_{i,j} - w_{i,j})^2}{w_{i,j}}$ and χ^2 by $\sum t_{i,j}$.

The computation yields the following values:

	two undamaged <i>Actinia</i>	one damaged <i>Actinia</i>	two damaged <i>Actinia</i>	
Slugs found with <i>Actinia</i>	$f_{1,1} = 30$ $w_{1,1} = 39.90$ $t_{1,1} = 2.46$	$f_{1,2} = 50$ $w_{1,2} = 52.64$ $t_{1,2} = 0.14$	$f_{1,3} = 53$ $w_{1,3} = 40.41$ $t_{1,3} = 3.92$	133
Slug not reaching <i>Actinia</i>	$f_{2,1} = 48$ $w_{2,1} = 38.10$ $t_{2,1} = 2.57$	$f_{2,2} = 53$ $w_{2,2} = 50.31$ $t_{2,2} = 0.14$	$f_{2,3} = 26$ $w_{2,3} = 38.59$ $t_{2,3} = 4.11$	127
	78	103	79	260

¹We are indebted to Ir J. J. BEZEM (Zoological Laboratory, Utrecht) and to Dr J. WESTENBERG (Zoological Station, Den Helder) for their kind assistance in this matter. The methods finally applied were all recommended by Dr J. HEMELRIJK, Mathematical Centre, Amsterdam.

And, finally, $\chi^2 = 2.46 + 0.14 + 3.92 + 2.57 + 0.14 + 4.11 = 13.34$.

Considering two degrees of freedom we find P about equal to 0.001. This value clearly indicates significance, so that we are allowed to assume that *Actinia*'s exert their attraction on *Aeolidia* strongest when they are damaged.

Secondly, we reconsidered our observations on the behaviour of *Aeolidia papillosa* (L.) with respect to hydroids. The following data were extracted from tables VI to X, pages 248-251.

	<i>Tubularia indivisa</i>	<i>Tubularia larynx</i>	<i>Laomedea flexuosa</i>	<i>Laomedea longissima</i>	<i>Hydractinia echinata</i>
Number of slugs reaching hydroids	17	7	4	5	8
Number of slugs reaching control aquarium	16	9	12	10	12

These figures seem to suggest that, once on the move, *Aeolidia* will tend to shun the hydroids.

For each hydroid species the numbers of the above table have been tested by means of the so called signtest (W. J. DIXON and A. M. MOON, The statistical sign test. Journ. Amer. Stat. Assoc. **41**, 556-566, 1946).

Application of this test did not reveal any satisfactory significance, so that repellent action of the hydroids has not been proved.

Thirdly, we investigated whether the slug *Cratena aurantia* (A. and H.) makes any difference between the hydroid *Tubularia indivisa* L. and *Tubularia larynx* Ell. & Sol.

The data in question were extracted from tables XVI to XXIII for *Tubularia indivisa* and *T. larynx* respectively.

<i>Tubularia indivisa:</i>	Positive reaction	No reaction
Table XVI.	245	44
„ XVII.	61	13
„ XVIII.	85	23
„ XIX.	30	17
„ XX.	143	28
Total	564	125
<i>Tubularia larynx:</i>	Positive reaction	No reaction
Table XXI.	178	138
„ XXII.	64	56
„ XXIII.	66	41
Total	300	235

The chi-squared test can here be applied to a 2×2 contingency table.

	<i>Tubularia indivisa</i>	<i>Tubularia larynx</i>	
Positive reaction	$f_{1,1} = 564$	$f_{1,2} = 300$	864
No reaction	$f_{2,1} = 125$	$f_{2,2} = 235$	360
Total	689	535	1224

For a 2×2 table χ^2 can be computed from the formula

$$\chi^2 = \frac{(f_{1,1} \times f_{2,2} - f_{1,2} \times f_{2,1})^2 N}{a \ b \ A \ B}$$

$$\text{This yields: } \chi^2 = \frac{(564 \times 235 - 125 \times 300)^2 \times 1224}{689 \times 535 \times 864 \times 360} = 93.04$$

Considering one degree of freedom we finally arrive at $P < 0.001$, so that we may conclude that *Cratena* distinctly prefers *Tubularia indivisa* to *Tubularia larynx*.

The other data are so convincing that we refrained from further statistical treatment.

TERRITORY AND THE REGULATION OF DENSITY IN TITMICE

by

H. N. KLUYVER AND L. TINBERGEN

Since the publication of HOWARD's "Territory in Bird Life" the behaviour aspects of territorial practice have been studied by many authors, but we are less well informed about its ecological significance. In particular, the presumed effect of territory upon density of population is still open to discussion.

Though he does not say so in so many words HOWARD (1920, p. 286) clearly assumes that for small passerines, territories have a minimum size beyond which the birds do not allow further crowding. In HOWARD's opinion, males which arrive in an area where the population has already reached this critical level will move around until they find unoccupied ground. If they do not succeed, they will be unable to breed.

On a priori grounds some limiting effect on the increase of local populations certainly is probable. It has been shown that the frequency of territorial quarrels increases with rising density (see e.g. HUXLEY, 1934; N. TINBERGEN, 1939, p. 70). Thus an important condition for a limiting influence is fulfilled, and such effect has been assumed by several authors (e.g. NICE, 1937; KLUYVER, 1951). But this thesis has not been supported by direct evidence, as LACK (1946) stresses.

The present authors have collected some information on this problem during bird census work in Dutch woods. In this paper we will show that density of population in the more attractive habitats is buffered to a certain extent. We will examine the possible explanations of this phenomenon, among which, in our opinion, HOWARD's thesis, is the most satisfactory.

KLUYVER's observations were made under the auspices of the Phytopathological Service, Wageningen. TINBERGEN did most of his work under the "Instituut voor Toegepast-Biologisch Onderzoek in de Natuur", Oosterbeek, and continued it at the Zoological Laboratory of the University of Groningen.

We have to acknowledge valuable help from many sources. Many of the Wage-

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I. CENSUS DATA

Between 1941 and 1952 TINBERGEN and his collaborators determined densities of Great Tits *Parus major*, Blue Tits *Parus coeruleus* and Coal Tits *Parus ater* in the woods near Hulshorst, Guelders Prov., Netherlands. In a number of characteristic sampling areas territories were counted by mapping singing males during early morning song. The method has been described in detail by L. TINBERGEN (1946).

The Hulshorst district consists largely of almost pure woods of Scotspine *Pinus sylvestris* with a rather poor bird fauna. Among these we studied a number of lots, varying in age between 35 and 70 years. Between these pinewoods are found narrow strips of mixed wood, 100 to 200 yards wide. For the greatest part these are situated on the borders of a small brook. These mixed woods are much more attractive to many species of songbirds than the pinewoods. Nevertheless, they are also of a comparatively poor type. Undergrowth of shrubs and herbs is scarce. The tree layer mainly contains oak *Quercus robur*, beech *Fagus sylvatica*, birch *Betula* spec., Scotspine, fir *Picea excelsa*, Douglas' fir *Pseudotsuga douglasii* and smaller numbers of *Quercus* cf. *rubra*, *Alnus glutinosa* and *Larix* spec. The tallest trees measure ca 60 feet.

In both the pinewoods and the mixed woods nesting sites are present in sufficient numbers. The land owner placed nest boxes in the pinewoods which otherwise would not provide suitable nesting holes for

Fig. 1. Number of breeding territories at Hulshorst. For comparison density figures for Apeldoorn (Apd) have been added, cf. text. 1 ha = 1 hectare = ca. 2.5 acres. NOTE. 1. The area covered in the pinewood counts at Hulshorst slightly shifted from year to year. On the average 100 hectares have been investigated each year for Great Tit and Coal Tit and 80 ha for Blue Tit. Average densities per 10 ha were the following:

	Great Tit	Blue Tit	Coal Tit
Mixed Wood . . .	5.6	6.8	5.0
Pinewood	1.46	0.83	2.18

2. The Apeldoorn counts are expressed in pairs per 100 nestboxes. In some years parts of the wood have not been investigated. On the average 177 boxes have been inspected in each year. The pinewood at Apeldoorn contains a small amount of deciduous trees. Average density of Great Tits is somewhat higher than at Hulshorst.

		MIXED WOOD HULSHORST	PINEWOOD HULSHORST	APD.	
		♂♂ ON 25.5 HA	♂♂ ON 100 HA		
GREAT TIT	1941	13½	18	1941	22
	1942	10	0	1942	7
	1943	13½	10	1943	24
	1946	14½	11	1946	24
	1947	14½	19	1947	28
	1948	17	11	1948	21
	1949	14½	23	1949	37
	1950	14	10	1950	22
	1951	15½	23	1951	—
	1952	17	21	1952	—
		♂♂ ON 9.7 HA	♂♂ ON 80 HA		
BLUE TIT	1941	5	3.5	1941	0.8
	1942	6½	5.2	1942	2.6
	1943	6	—	1943	7.6
	1946	9	6.1	1946	6.1
	1947	6	4.7	1947	4.5
	1948	7	10.8	1948	11.6
	1949	7½	11.7	1949	11.8
	1950	6	4.0	1950	4.9
	1951	5½	3.5	1951	—
	1952	8	9.6	1952	—
		♂♂ ON 25.5 HA	♂♂ ON 100 HA		
COAL TIT	1941	14½	34	1941	7.2
	1942	14½	36	1942	10.5
	1943	22	45	1943	16.7
	1946	10	11	1946	7.6
	1947	12½	19	1947	6.0
	1948	13½	19	1948	9.8
	1949	13	16	1949	7.3
	1950	10	13	1950	0.6
	1951	9½	13	1951	—
	1952	7½	12	1952	—

Fig. 1.

Great Tits and Blue Tits. The mixed woods contain a great number of natural tree holes and moreover some nest boxes.

Density figures for mixed wood and pinewood are summarised in Fig. 1. In the first place, density per unit of area in the mixed wood was always much higher than density in the pinewood. This applies to all three species of titmice. Apparently they have a pronounced preference for the mixed wood.

Furthermore, fluctuations from year to year are much smaller in the mixed wood than in the pinewood. This is clearest in the Great Tit. In this species density in the mixed wood fell to 10 in 1942 whereas in all other years it fluctuated only between $13\frac{1}{2}$ and 17. The pinewood, on the other hand, had no Great Tits at all in 1942 and in the other years its population varied between 10 and 23. Apparently density in the mixed wood is buffered in some way.

This effect can be demonstrated more conveniently by plotting year for year density in the mixed wood against the accompanying value of density in the pinewood (Fig. 2A). Instead of proportionality between both figures (resulting in a straight regression line cutting the origin of the graph) one finds the points grouped on a line almost parallel with the abscissa. Thus, as density in the pinewood increases, density in the mixed wood remains almost constant. Nevertheless, it is clear that the regression line eventually must reach the point 0-0. So in its complete form it will include a part steeply rising from the origin to point 1942. This part has been extrapolated on Fig. 2A.

Density in the pinewood is an approximate index of total population in the Hulshorst district, as the mixed wood covers only a very small part of this area. Thus a gradual increase in total population hardly raises density in the mixed wood except during the very first step of the process which we only know by extrapolation.

In the Blue Tit the correlation graph for density mixed wood and density pinewood shows a slightly different picture (Fig. 2E). Unfortunately the regression line cannot be drawn very exactly as the point 1946 fits badly. It is clear, however, that it has no horizontal part like in the Great Tit. Nevertheless, density in the mixed wood increases more slowly than density in the pinewood, at least within the range of observations. So we can speak again of a buffer effect. We are inclined to explain the abnormal values for 1946 as a chance effect in sampling, but we cannot prove this.

In the Coal Tit finally the situation is not quite clear. As compared with the other years, the points of high density (1941, 1942 and 1943; Fig. 2B) strongly suggest a buffer effect. Unfortunately, however, the

later years have not given the opportunity of rechecking the distribution at high general density. In this period Coal Tits always have been scarce.

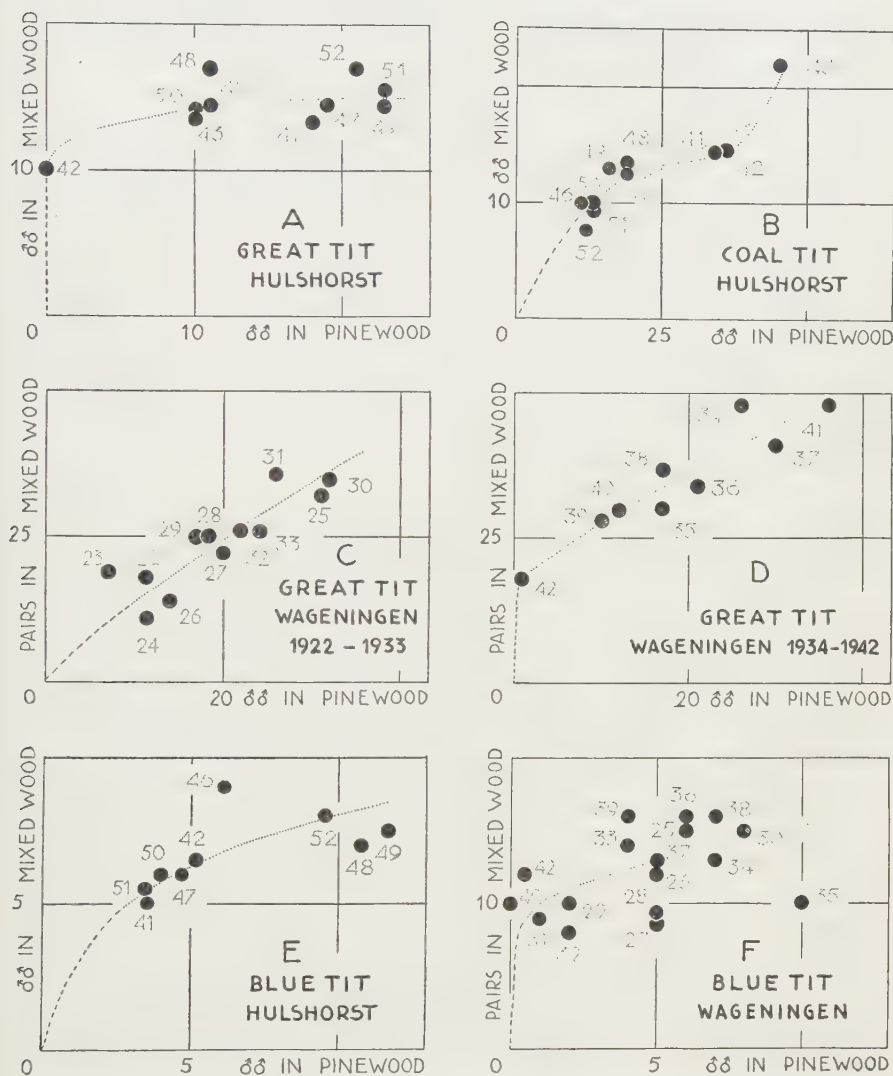


Fig. 2. Relation between numbers of titmice in mixed wood and in pinewood. Data from Fig. 1 and Table I. Regression lines drawn at sight. Dotted: years of observation.

The observation points show only slight deviations from a straight line cutting the ordinate near point density mixed wood = 7, but the

most probable interpretation seems to us a regression line rising through points 1950 and 1951 to points 1947 and 1948, bending in horizontal direction to points 1941 and 1942 and finally rising again to point 1943. A tentative explanation for point 1943 is given on p. 281. So only between density (pinewood) 8 and 15 density in the mixed wood would be buffered.

The total population of these species of titmice apparently strongly fluctuated in the Hulshorst district. These fluctuations occurred almost synchronously in a much larger area. Through the kindness of the late A. J. SCHRAVENDIJK, of L. J. KRAMER and A. J. VEGTER we can present population figures for the "Berg en Bos" wood near Apeldoorn, 15 miles SE from Hulshorst. As at Hulshorst, pinewoods dominate in this estate. The data have been included in Fig. 1. In general they show a similar trend as those for the pinewoods at Hulshorst. Thus the Great Tit minima for 1942, 1946, 1948 and 1950 were also found at Apeldoorn. The same holds good for the Blue Tit peak of 1948-1949 and the Coal Tit peak of 1943.

At Wageningen (Guelders Prov.) KLUYVER collected a much longer series of observations on the estate "Oranje Nassau's Oord".

The woods of this estate are poor in natural nest holes. Nearly all Great Tits and many Blue Tits therefore nest in boxes, which form almost optimal nesting sites for these species. Except in the years 1930-1933, boxes were present in excess throughout the estate. The number of first broods in these boxes was recorded year after year and these figures are used here as an index of population (Table I).

Great Tit. The Wageningen area comprises mixed wood as well as pinewood, the mixed wood being on the whole younger than that at Hulshorst, but richer in tree species. It has about the same average density of Great Tits. In earlier years, however, its vegetation was much poorer. This is clearly reflected in the census data (table I). Between 1922 and 1933 the density of Great Tits in the mixed wood was almost equal to that in the pinewood, but from 1934 onward it averaged about twice as much. Thus the Great Tits showed a clear preference for the mixed wood during these latter years but not during the earlier.

The change in 1934 was sudden. This has the following explanation. After 1930 the younger mixed plantations (which started as undergrowth in the older wood) had grown so far that they became a suitable habitat for Great Tits. There was, however, a shortage of nesting sites since there were only a few nestboxes. This situation changed in 1934, when more boxes were provided and the tits were enabled

to utilise the young plantations fully. The attractiveness of the mixed part of the estate therefore increased abruptly.

The pinewood at Wageningen differs from most of the pinewoods at Hulshorst in having some shrub growth and taller trees. The average density of Great Tits is much higher than the average at Hulshorst.

TABLE I

Numbers of breeding pairs at Wageningen (Oranje Nassau's Oord) in 60 hectares of mixed wood and in 61 hectares of pinewood.

Year	Great Tit (<i>Parus major</i>)		Blue Tit (<i>Parus caeruleus</i>)	
	Mixed Wood	Pinewood	Mixed Wood	Pinewood
1922	18	11		
1923	19	7		
1924	11	11		
1925	32	31	15	6
1926	14	14	12	5
1927	22	20	9	5
1928	25	18	9	5
1929	25	17	10	2
1930	35	32	15	8
1931	36	26	9	1
1932	26	22	8	2
1933	26	24	14	4
Av. 1922-1933	24.1	19.4	—	—
1934	48	26	13	7
1935	30	17	10	10
1936	34	21	16	6
1937	41	30	13	5
1938	37	17	16	7
1939	28	10	16	4
1940	30	12	10	0
1941	48	36	no observations	
1942	18	1	12	1
Av. 1934-1942	34.9	18.9	—	—
Av. 1925-1942	—	—	12.2	4.6

There, the old, well grown pinewoods have an equally dense population, but these are scarce and the average for the district depends mainly on the density of younger and slowly growing woods, which is low. Apparently the type of pinewood which prevails at Wageningen, is more attractive to Great Tits than the lower woods at Hulshorst.

In Fig. 2C and 2D density in the mixed wood at Wageningen is correlated with density in the pinewood. In the years 1922-1933, when mixed wood and pinewood were almost equally attractive to Great Tits, density in the mixed wood was directly proportional to density in the pinewood. This is shown by the regression line which passes

through the origin of the graph. But from 1934 onward, when the mixed wood became more attractive than the pinewood, the relation clearly changed. The regression line for this period, when drawn as a straight line, does not cut the origin. Density in the mixed wood changed much more slowly than density in the pinewood. Thus we can speak again of a buffer effect, present since the time when the attractiveness of the mixed wood had increased. It should be noted, however, that the regression line for 1934-1942 has no horizontal part as at Hulshorst, so that the buffer effect was less pronounced at Wageningen than at Hulshorst.

Blue Tit. The observations are summarised in Table I. In several respects they differ from those on the Great Tit. In the first place density in the mixed wood always was much higher than density in the pinewood and even in the years before 1934 the Blue Tit preferred the mixed wood. This in our opinion reflects the fact that the Blue Tit has a stronger preference than the Great Tit for deciduous wood.

There is another difference between the figures for Blue and Great Tits. Between 1913 and 1924 density of Blue Tits in both the mixed wood and the pinewood was much lower than in the years after 1924. Since a similar increase was noted at other localities, we assume a general rise of the population of Blue Tits which was not caused by local conditions.

We shall analyze only the period 1925-1942, since the numbers in the earlier period were too small. In Fig. 2F density in the mixed wood is compared with density in the pinewood. The result is similar to that in the Great Tit 1934-1942. Density in the mixed wood is not proportional to density in the pinewood. It is already rather high when density in the pinewood is low. As the numbers in the pinewood rise, density in the mixed wood increases relatively slowly. Apparently the density of Blue Tits too was buffered in the mixed wood at Wageningen.

II. THE "BUFFER MECHANISM" IN THE GREAT TIT

Both at Hulshorst and at Wageningen densities of Great and Blue Tits were high in attractive mixed woods and low in neighbouring pure stands of Scotspine. Fluctuations from year to year were small in the former habitat and considerable in the latter. As the total population in both mixed woods and pinewoods increased, density in the mixed wood rose much more slowly than density in the pinewoods. This buffer effect was very pronounced in the Great Tit at Hulshorst and in the Blue Tit at Hulshorst and Wageningen. The Great Tit records for Wageningen show it in a less marked but nevertheless convincing form.

Here the effect only occurred in the period when the mixed wood was rather attractive for the tits. Finally observations on the Coal Tit in Hulshorst suggest similar relations in this species.

We must now examine the mechanism which buffers density in the mixed woods. This requires knowledge of the life history of the different species. At present, only the Great Tit has been studied in detail. We will therefore first confine our attention to this species.

It may be useful first to summarise certain aspects of the Great Tit's biology. The phenomena of dispersal especially interest us here. KLUYVER (1951) has studied these subjects in the woods near Wageningen already described in this paper, and we shall chiefly summarise his findings.

Ringed data show that a considerable number of Great Tits select a home range in autumn and early winter of the first year of life. After reaching this age many but not all Great Tits are very faithful to their homes¹. Generally speaking the further life of these individuals is confined to a range of about 50–80 hectares. The nucleus of this range is the area where the individual roosts during autumn and winter and where it breeds in successive summers; it has a surface of ca. 10 hectares. This area is named the "domicile". It should be noted that the domiciles of different individuals overlap to a considerable extent. So they certainly are not comparable with territories.

In early autumn (especially September) there is much fighting and threatening among Great Tits. Both males and females participate in these quarrels which often occur on fixed spots. We are inclined to explain them as territorial fights, but we cannot prove this.

Aggressive behaviour is suspended in winter. During this season the birds roost in the domicile, but they spend the day in its larger surroundings, which, as already mentioned, do not cover more than ca. 50–80 hectares. The tits then flock together in the well known mixed parties. These scatter at dusk; every Great Tit then moves to its own domicile to roost.

The defence of territories can already be observed in late winter. BRIAN (1949) found that the boundaries between neighbouring territories were still rather vague in February. They become sharper in the course of spring, at least in densely populated areas like the mixed woods studied by us. In gardens at Wageningen, where the population of Great Tits is still denser, the boundaries between territories were very sharp, though they shifted slightly from one week to another. On the other hand fights between neighbouring pairs regularly were seen at low densities in the pinewoods. Here, however, the boundaries were not sharp.

¹ The same has been found by PLATTNER and SUTTER (1946).

At least in the mixed woods which we studied, the whole area is divided into territories during spring. For the pinewoods this is uncertain.

Within their domicile individual Great Tits do not inhabit exactly the same territory in successive springs; as a rule there is some shifting.

Many Great Tits are faithful to the domicile which they select in their first autumn. This fixation, however, is not absolute. For instance, when a habitat suddenly becomes very unsuitable by the cutting of trees or the removal of nestboxes, many tits will leave it. In such cases it was found that some of them move over considerable distances.

Displacements also occur under more normal conditions. In the mixed wood at Wageningen there is a category of birds which appear in autumn and emigrate in spring. In some winters this group is as numerous as the residents, in others they are scarce.

It is not known where these birds settle in spring. Some of them might be true migrants, which have wintered at Wageningen, but others probably do not go far away. It is possible that the latter settle in unattractive habitats, e.g. in the poor pinewoods. In this type of habitat regular observations of ringed birds were not made. Winter counts in poor pinewoods at Hulshorst revealed an increase of Great Tits in early spring, but this does not exclude other explanations.

Summarising we find that the distribution of Great Tits over different breeding habitats takes place in two phases. In rough outline it is already determined in autumn when many individuals settle in their final domiciles. In detail, however, it takes place in early spring when the breeding territories are established. Many birds remain faithful to the domiciles which they select in their first autumn of life. Nevertheless displacements at greater age do occur. There is, for example, a regular emigration from the mixed wood during late winter or early spring.

After this introduction, we can deal with our main point: the factors buffering density in the mixed woods.

In principle, density at a certain locality is determined by three main processes: reproduction, mortality and habitat selection (in a broad sense). We will discuss the possible influence of each of these factors in the buffer mechanism.

REPRODUCTION

The Great Tits of the mixed woods do not form isolated populations which depend on their own reproduction for the recruitment of a new generation. Before settling the young birds may move over consider-

able distances (KLUYVER, 1951). The latter are much greater than the dimensions of our mixed woods. Moreover the Wageningen ringing data show that birds which were born in the mixed wood often settle in pinewoods and vice versa. KRÄTZIG found the same exchange between richer and poorer habitats. So eventual differences in reproduction rates between the pairs of mixed woods and those of pinewoods cannot account for the differences in density between both habitats, nor for the observed buffer effect.

MORTALITY

As we have seen, the rough distribution over different habitats has already taken place in autumn. Therefore we must examine, how far mortality between autumn and spring can contribute to the buffer effect.

At first sight the remarkable distribution in 1942 might reflect an influence of mortality. In this year density in the mixed woods was 50–70 % of the average value, but density in the pinewoods fell to 0–7 % of the average. The winter 1941–'42 was very hard. It seems possible that the autumn population in 1941 was more or less normal in both mixed woods and pinewoods and that birds which had their domicile in pinewood suffered much more from frost and snow than those which had domiciles in the mixed wood.

Such differential mortality could operate either during roosting at night or by day. In the pinewoods at Hulshorst and at Wageningen most Great Tits roost in nestboxes, but in the mixed woods many make use of holes in trees. Possibly nest boxes are colder in winter nights than holes in trees. This might account for a difference in mortality. But inspections of nestboxes during and after the winter never revealed a significant number of dead titmice. Therefore we cannot accept that the disappearance of Great Tits in the pinewood was caused by a high mortality of the birds which roost in this habitat.

During daytime, on the other hand, many of the tits which have domiciles in the pinewood live under the same conditions as those which have domiciles in the mixed wood. This is especially noticeable at Hulshorst, where the width of the mixed wood is 100–200 m whereas the diameter of the range in which the birds wander each day is at least 650 m. (This figure is derived from the Wageningen ringing data; KRÄTZIG (1939) found much higher figures.) This implies that all birds which have domiciles in the mixed woods at Hulshorst may spend a great part of the day in pinewood. On the other hand many birds roosting in pinewood may visit the mixed woods. In fact, flocks which move from the pinewood to the mixed wood and the other way round

were often observed. At Wageningen the birds seem to concentrate in the mixed wood during winter days. At least, feeding shelves in the pinewood did not attract Great Tits whereas feeding shelves placed in the mixed wood were visited by birds roosting in the mixed wood as well as by birds roosting in the pinewood.

It seems probable that the mixed wood offers better conditions of food and cover during winter. These better conditions, however, are not the exclusive privilege of the birds which roost in the mixed wood. Many inhabitants of the pinewood share in them.

Also by day an influence of mortality is, therefore, unlikely. Hence the spring densities of 1942 probably do not reflect differential mortality.

Putting the question more generally, we must examine whether mortality could ever produce the buffer effect. We now meet a serious difficulty: we should know autumn densities and these have not been recorded. Theoretically, however, four possibilities can be distinguished.

- A. Autumn density in both habitats has a constant value from year to year and the buffer effect is produced by winter mortality.
- B. Autumn density fluctuates in both habitats.

- 1. Autumn density in the mixed wood is not buffered and consequently directly proportional with autumn density in the pinewood. The buffer effect is produced by winter mortality.
- 2. Autumn density in the mixed wood is not buffered. The buffer effect is produced by movements of the birds from one habitat to the other during spring.

- C. Autumn density in the mixed wood is already buffered whereas it fluctuates in the pinewood. The buffer effect is produced by movements of the birds during dispersal in early autumn.

In the two last mentioned possibilities habitat selection is the essential factor. Hence these will be discussed in the next section. We must examine here whether one of the first two possibilities can explain our observations.

A. Autumn density in both habitats has a constant value from year to year. A buffer effect could result if winter mortality of birds roosting in the mixed wood fluctuated between much narrower limits than winter mortality of the pinewood birds. This hypothesis can be rejected because the number of birds in autumn certainly is not constant in both habitats. Superficial observations in autumn already reveal huge differences in general density between one year and the next. Moreover, counts in late autumn show similar fluctuations. In a definite part of the mixed wood at Wageningen the following numbers of Great Tits have been recorded during nightly inspections of nestboxes

in early December: 1936 59, 1937 71, 1938 110, 1946 88, 1947 43, 1948 88, 1949 77, 1950 83, 1951 98.

B (1). The number of birds which during autumn have a domicile in the mixed wood is not buffered but directly proportional with the pinewood population. A buffer effect will occur if winter mortality percentage in the mixed wood is density dependent, whereas in the pine wood it is not or to a smaller extent. To formulate this condition in a more general way: a buffer effect will result if the difference "percentage winter mortality in mixed wood less percentage winter mortality in pinewood" has increasing values with increasing density of population.

A strong argument against this hypothesis was already put forward. During winter birds roosting in the mixed woods are exposed to almost the same conditions as birds which roost in the pinewoods. Therefore, a great difference in mortality is not probable.

In our further discussion of this hypothesis we will treat the Hulshorst and the Wageningen data separately. For Hulshorst this hypothesis would include that winter mortality always leaves an almost constant number of survivors in the mixed woods. This seems only possible if mortality depended entirely on the following mechanism: the mixed wood has a fixed number of safe sites and all individuals which do not occupy such a safe site are killed. At first sight this seems very improbable, but in the case of the Great Tit the number of roosting holes could operate in this way as a limiting factor. Roosting holes, however, are present in great excess in the mixed woods at Hulshorst. We therefore cannot accept that the buffer effect at Hulshorst is produced by differential mortality.

As an alternative hypothesis one could assume that the number of safe sites in the mixed woods is constant because the supply of food is the same from year to year. Even if we neglect the fact that birds roosting in the mixed wood collect a great deal of their food in the pinewood, this relation cannot exist. In the first place, winter food density certainly is not equal from year to year (see below, p. 279). In the second place, even if it was equal, the postulated effect would not occur. In winter the accumulation of new food almost stops. So the birds mainly depend on a stock of food which is present already late in autumn. Now our starting point was that autumn density of tits fluctuates. Hence in a year with many birds the stock of food would decrease in a much faster way than in a year with few birds. Instead of equal numbers of survivors, few of them should be expected in the former year and many in the latter. Hence, if the number of birds in autumn fluctuates – which happens – even a constant amount of food in the mixed wood would not lead to a constant number of survivors in spring.

At Wageningen, on the other hand, the situation is different from that at Hulshorst. Here the number of survivors in the mixed wood is not constant, although it is buffered. Hence the argument, which was given for Hulshorst, cannot be followed in this case. Nevertheless, the hypo-

thesis put forward in this section most probably does not explain the Wageningen data. It postulates a sharp correlation between winter mortality and population density in the mixed wood. The data of KLUYVER (1951) do not suggest such a marked correlation. An effect of density on mortality could be deduced only for severe winters (p. 125) and the estimates of the yearly mortality rate in adult birds (p. 100) do not point to a correlation with density at all. Thus the main condition for the hypothesis seems not to be fulfilled at Wageningen.

Summarising this section we consider it very improbable that mortality buffers density of Great Tits in the mixed woods at Hulshorst and at Wageningen.

HABITAT SELECTION

In the preceding pages we found no reasons for assuming that either reproduction or mortality produce the density phenomena which we described. There remains only the alternative that the buffer mechanism is a component of habitat selection. We explain the census data for Hulshorst essentially in the following way: the mixed woods are "filled up" to a critical level and not further. The excess birds settle in the pinewoods. In some years, these are many, in others few.

At Wageningen, on the other hand, a fixed level of critical density cannot be distinguished but here as well the percentage of birds which settle in the pinewood increases as total population reaches higher values. A more detailed discussion of the Wageningen data will be given further below. We will first restrict our attention to the Hulshorst data.

One could give the following tentative explanation for the state of affairs at Hulshorst. Some element in the habitat, which every bird requires, is present in limited and constant supply in the mixed wood. Although many hypotheses can be made about the nature of this element, only two possibilities seem reasonable: the number of roosting holes and/or the number of nest sites is limited. Neither is the case, however. As already stated the mixed wood at Hulshorst contains a great number of tree holes (which are suitable for both roosting and nesting) as well as some nest boxes. Moreover, if the number of holes were to limit the population, this influence could be expected to act upon the numbers of Great Tits and Blue Tits taken together, because the latter species uses similar holes as the former. In other words, one would expect that only the combined population of Great and Blue Tits would be buffered. The percentage in which each species is represented in this sum would fluctuate in dependence on its general abundance. This clearly is not the case. The number of Great Tits

in the mixed wood is almost constant despite big differences in the ratio Great Tits: Blue Tits as calculated for the district as a whole.

Other assumptions, viz. that the conditions of cover or the amount of food limit in a similar way density of the mixed wood, easily can be dismissed. Cover conditions are good throughout the mixed wood. That food supply in this habitat would attract a fixed number of Great Tits in every year seems completely improbable. In the first place the density of food varies very much from year to year. To mention one example: in the mixed wood beech mast is an important food item during the cold season. In some years it is present in enormous excess, in others it hardly can be found. In the second place, the total number of birds which seek a home is rather variable from one year to another. Even if food supply were constant and limited in the mixed wood, a great number of birds would be attracted by it in years of high population and a small number in years of low population.

So we cannot accept that the constant level of population in the mixed wood at Hulshorst is caused by the fact that the supply of things which the birds require is limited and constant in this habitat. In our opinion there is only one reasonable alternative hypothesis namely, that the density of population of the same species is a factor in habitat selection. We assume that birds which seek a home are guided by two counteracting tendencies: a preference for mixed woods as such and an aversion from densely populated localities. Birds which settle early will choose a place in the mixed wood. The more this is filled up, the less attractive it will be for other individuals. In these circumstances, the latter will prefer a habitat which per se is less attractive, but where no dense population is present. Thus as the number of individuals in the district rises, there will be an increasing disposition to settle in the pinewoods.

This hypothesis implies that density in the mixed wood will increase until the attractiveness of the habitat is counterbalanced by the repelling influence of population already present. Therefore, we can expect that density in the mixed wood will rise to a certain critical level, a "level of saturation", and not further.

That in the Great Tit many adult individuals are faithful to the domicile of the preceding year forms no serious objection against our explanation. It only means that those adults which survived already occupy part of the positions when new birds try to settle.

The next question to discuss is, in which season does the repelling influence of population density operate?

We have seen that there are two phases in habitat selection: in autumn many Great Tits settle in their domiciles, and in spring the final breeding territories are established. These are counted in our censuses. We know further that part of the birds, which have settled in autumn, are killed during winter and that others emigrate in early spring.

In principle the density effect could operate in one of the two phases of dispersal or in both. We can deduce, that it works at least in spring, but we have no observations which allow a conclusion about the autumn period.¹

If the density effect does not operate in spring, we have to assume that it is restricted to the autumn. In winter, however, many birds die. Of course this winter mortality cannot be equal year after year. Thus the number of survivors would fluctuate from one year to another. This is in contradiction with the census data for Hulshorst, which show very small fluctuations. We therefore must conclude that the density effect works at least in spring. This implies that the birds are redistributed to a certain extent during this season.

Unfortunately, we have no conclusive information on this redistribution. In principle, it might imply either an emigration from or an immigration into the mixed wood. It seems probable that movements in both directions may occur. When the total population has decreased very much during winter (as in 1942), we must assume a displacement from the pinewood into the mixed wood. On the other hand, in years with a more normal density the Wageningen ringing data show that part of the population emigrates before spring from the mixed wood. This suggests that in autumn or winter the mixed wood is filled beyond the saturation level and that excess birds disappear. Although it is very probable that true migrants are scarce among these emigrating birds (KLUYVER, 1951 p. 31) we do not know whether the latter move into the neighbouring poor habitats. These movements need to be studied more intensively before we can state whether they contribute to the buffer effect.

• We should add here that spring densities in the mixed wood can be adjusted to a certain extent by local movements of birds which do not leave their original domiciles. We have seen that the domicile has a larger surface than the average territory. Thus birds living on the borderline between mixed wood and pinewood can select either habitat for their final breeding territory. Especially at Hulshorst, where the mixed woods are narrow strips, 1–2 territories wide, this factor might have considerable influence.

Finally, it should be stressed that besides displacements from the mixed wood to poorer habitats and the other way round, there also might be an exchange between mixed woods and still more attractive habitats.

We now must consider whether the critical level or "level of saturation" is the same in all types of habitat. In our hypothesis we supposed that the critical level represents the density value at which, according to the innate standards of the bird, the attractiveness of the habitat is counterbalanced by the repelling influence of population density. Certainly, the attractiveness of different habitats is not equal. Thus we can expect the critical level to be low in unattractive habitats and high

¹ KLUYVER (1951, p. 122–123) brought forward evidence for large scale emigrations of juveniles in autumn. His data strongly suggest, that these emigrations are density-dependent. It is not known, however, whether these displacements influence density in the mixed wood to a greater extent than density in the pinewoods, in other words whether they contribute to the buffer mechanism or not.

in attractive ones. This in fact seems to be true. Parts of the woodland district at Hulshorst have a still denser population of Great Tits than the mixed woods. These are among others the gardens near houses. Apparently this habitat is still more attractive to Great Tits than the mixed woods. As the latter are saturated in most years, the former must also be filled up to the critical level. This consequently is higher than the critical level in the mixed wood. Apparently these gardens are so attractive, that the birds which inhabit them endure more members of their own species than do the birds which live in the mixed woods.

On the other hand, the pinewoods are clearly less attractive to the tits than the mixed woods. Therefore we may expect that here the critical level is lower.

Hence the important question arises, what happens when the pinewoods are also saturated to the critical level. There are no poorer habitats which then may harbour the remaining birds. There are then two alternatives: the birds may attempt to settle in any of the already saturated habitats or they may not settle at all. At present we cannot give a definite answer to this question.

If we were to assume that our explanation could also be applied to the Coal Tit (which is not proven, see below), we have one observation which might throw some light on this problem. In 1943 the population of Coal Tits at Hulshorst was very high. As compared with 1942 both the mixed woods and the pinewoods had a remarkable increase in density. This might indicate that the saturation level in pinewood was passed and that the excess birds settled in all the habitats. If this interpretation is right, population density in the mixed woods is only buffered as long as the pinewoods are undersaturated. Therefore an effect on the total size of population would be doubtful.

So far we have considered only the census data for Hulshorst. At Wageningen density of population in the mixed wood (1934-1942) was buffered to a certain extent, but it was not as stable as at Hulshorst. Nevertheless we believe that the Wageningen data must be explained in the same way as those for Hulshorst. The argument on p. 277 makes it very probable that at Wageningen too, the buffer effect is a product of habitat selection. An influence of limited supply of nestboxes or a food influence (see p. 278) seems hardly probable. Hence we assume again an influence of density in habitat selection.

Three factors might explain why density in the Wageningen mixed wood is not buffered to the same extent as at Hulshorst.

1. The difference in attractiveness between mixed wood and pinewood is smaller at Wageningen than at Hulshorst (cf. p. 270). Now it is evident that our suggested principle will be the more effective, the greater the difference in attractiveness between "rich" and "poor" habitat. Where the latter is very unattractive, the birds will do their

utmost best to find a place in the former, and there will be a strong tendency to fill this up to the saturation level. The tendency will be weaker when the poor habitat is still fairly attractive, like the pinewood at Wageningen. In such case we cannot expect that the mixed wood will be filled till the exact limit of tolerable density. It therefore seems quite natural that density in the mixed wood at Wageningen was not buffered to such extent as at Hulshorst. In this regard the older series at Wageningen (1922-1933) is of interest. In these years there was hardly a difference in attractiveness between mixed wood and pinewood. Accordingly, there was no buffer effect at all.

2. At Wageningen, habitats which are still more attractive than mixed woods cover a relatively larger area than at Hulshorst. In years of low total population, this might imply that the mixed woods are not filled till the critical level. We do not know whether this factor has real significance.

3. In relation to its surface the mixed wood at Wageningen has a relatively shorter borderline than the mixed wood at Hulshorst. We have mentioned the possibility that birds living at the borderline move from one habitat to the other without leaving their domicile. This might be an important factor in the regulation of density in the mixed wood. The shorter borderline would lessen the effectiveness of this factor at Wageningen.

The differences between Wageningen and Hulshorst suggest that local conditions at Hulshorst favour the operation of the density effect in habitat selection. Further investigations will have to show, to what extent local conditions may obscure it. We have shown the phenomenon to exist, but we cannot give an exact delimitation of its influence. Thus in several regards our observations invite further research. In the first place, more observations of density in attractive and unattractive habitats are desired. Further density measurements in autumn and winter would be very welcome. Finally a large scale investigation of the movements of individuals from one habitat to another is very much needed.

We have concluded that the density effect in habitat selection operates at least in spring. We must examine now by what elements of behaviour it is produced. It might be caused by aggressive action, by avoiding behaviour or by both. Now both are essential features of territorial practice, which is at a peak in spring. Therefore, we accept as the simplest explanatory hypothesis that the population effect in habitat selection is an immediate consequence of territorial behaviour. The Great Tit is a territorial bird, and in spring the mixed wood is

divided completely into territories. The buffer effect implies that the size of these territories does not decrease in proportion with a rise in total population, but more slowly. It seems justifiable to regard this total population as a more or less exact expression of the number of birds which try to settle in any given year. At Hulshorst a marked increase in this number hardly lowered the average size of territories in the mixed wood. At Wageningen a definite minimum size of territory was not reached, but the decrease was relatively small.

When speaking more generally, it is of course not necessary to postulate such a relation with territorial practice. A similar effect could be reached when animals were only mutually hostile (without settling at an individual territory) or when they merely avoided each other.

The above explanation implies that we accept Howard's principle for the populations of Great Tits, but under restricted conditions. In the first place it should be added that the limit of compressibility of territories is not the same in every habitat. Further we conclude that this principle can buffer density in attractive habitats only as long as the population in less attractive environments of the same district has not yet reached the "level of saturation". We do not know what happens when more birds are present.

We should stress here that we realize we have not provided a direct proof for HOWARD's thesis. Such proof would require much more knowledge about behaviour and movements of individual birds than we have at present. We feel, however, that the facts reported here are most easily explained by Howard's hypothesis.

III. THE "BUFFER MECHANISM" IN THE BLUE TIT AND THE COAL TIT

Very little can be said about the buffer mechanism in the two other species, as their life history has not been studied sufficiently. We can conclude that the census figures are not in contradiction with the explanation which we gave for the buffer effect in the Great Tit. (A tentative explanation for the abnormal values for Coal Tit 1943 has been given on p. 281). It is impossible, however, to exclude in a strict way the alternative hypotheses discussed on p. 274-278. We may add that both the Blue Tit and the Coal Tit defend territories.

IV. DISCUSSION

The census data, presented in this paper, show that density of population in three species of titmice was buffered to a certain extent in densely populated mixed woods and fluctuated much in neighbouring

pinewoods, where the population was low. KRÄTZIG (1939, p. 32) has found the same phenomenon. Referring to Great Tits he writes about the favourable habitats: "dass diese Typen offenbar wegen ihrer stärkeren Laubholzdurchmischung als Siedlungsgebiete bevorzugt werden. Es sind dieselben Waldteile, die auch zahlenmässig nur geringe jährliche Siedlungsveränderungen aufweisen..." and he adds that density in the neighbouring poorer habitats clearly sinks in unfavourable years.

Before KRÄTZIG, ERRINGTON (1934, 1943) and ERRINGTON and HAMERSTROM (1936) described similar relations in other species. According to these authors Bobwhite Quails (*Colinus virginianus*) and Muskrats (*Ondatra zibethica*) have a more or less constant density in the most attractive habitats whereas poorer sites are only occupied in peak years. Finally, the observations of SOUTHERN and MORLEY (1950) suggest analogous conditions in the Marsh Tit (*Parus palustris*).

When examining the nature of this buffer mechanism, we have concluded that at least in the Great Tit density of population is an important factor in habitat selection. We assume that the birds have an aversion for densely populated localities. Such a population effect in habitat selection has been suggested in several other cases.

For instance, ERRINGTON (l.c.; 1946) assumes it in his explanation of the regulation of density in Bobwhite Quail and Muskrat. SIIVONEN (1941) supposes the same factor as releaser of mass emigrations in the Waxwing (*Bombycilla garrulus*). Finally CROMBIE (1944) in his experiments with grain boring insects found a pronounced correlation between population density and the intensity of emigration among the larvae of *Rhizopertha dominica* and *Sitotroga cerealella*.

In the Great Tit movements of individuals seem to play an important rôle in the regulation of density. KLUYVER (1951) assumes that the emigrations of juveniles in autumn chiefly radiate from densely populated areas. In this paper we have postulated movements in spring which adjust density in the more attractive habitats. These findings support ERRINGTON's view that displacements and the innate standards of tolerable crowding are important factors in density regulation among higher vertebrates.

We found reasons to suppose that at least in spring the density effect in habitat selection of Great Tits is produced by territorial behaviour. Although for definite proof more observations of behaviour are required, we accept HOWARD's thesis as the most satisfactory explanation. So we assume that more birds settle in the pinewoods as territories in the mixed wood approach the limit of compressibility.

We concluded that this limit is not equal in all kinds of habitats but varies in relation with the attractiveness of the latter. During our

observations the limit was never reached in the unattractive pinewoods. So we do not know, whether HOWARD's principle still works when density in the poor habitats has reached the critical level. Probably the latter condition generally is prevented by the above mentioned emigrations in autumn.

As far as concerns these autumn emigrations it is still unknown whether they have relations with territorial practice. In fact, there is a marked rise in hostility during the fall, but it is not certain whether real territories are established. A thorough study of autumn behaviour in ringed birds would be very valuable.

According to our assumption Great Tits are guided during habitat selection by two counteracting tendencies: a preference for certain habitats and an aversion for densely populated localities. The distribution over different habitats therefore is not the effect of habitat preference only, but of both dispositions.¹

The biological significance of this principle of density regulation becomes clear, when we ask, what would happen if the birds were guided only by their preference for certain habitats and not by their aversion for crowding. The population then would be concentrated almost exclusively in the attractive habitats. When the population increased the densities of birds in these attractive habitats would become very great. We know that such concentrations of animals are in general unstable. There would follow an unfavourable trend in the rates of reproduction and mortality, eventually accompanied by an exhaustion of the resources of the habitat. On the other hand the surrounding unattractive habitats would be utilised to a very small extent. In the long run the species in question could only maintain a much smaller population than it does in reality. Thus the interaction of habitat preference and the aversion for concentrations prevents the development of topheavy populations in favourable habitats and ensures the utilisation of less attractive environments. The fact that individuals avoid concentrations probably will favour their survival.

This is a rather vague statement, based only on general ecological principles. But we cannot go further than this. At present we do not know at what densities the populations of the favourable habitats become "unsafe". Neither do we know whether shortages of food or some other factor (e.g. an increased risk for predation or disease) would dominate in such unfavourable development. So the hypothesis of the

¹ This point seems of importance for the interpretation of the results of bird censuses. It implies that the ratio of densities in different habitats is not a simple expression of the degree to which the birds prefer one to another. We think it probable that this effect is not restricted to the Great Tit, but is found in other species as well.

food value of territory (which is often linked with the thesis that territory limits the population) remains untouched in this study.

In its effect on survival the buffer mechanism has some resemblance to the emigrations of Lemmings and, probably, with similar but less conspicuous phenomena in several other species. The Lemming emigrations lower the density in favourable habitats which are heavily populated. Moreover part of the animals which emigrate find suitable habitats, which they otherwise would not have reached (KALELA, 1949). On the other hand, these emigrations do not start until the density in the favourable habitat has already reached a very dangerous level. Hence this regulation is less effective than that in the Great Tit, where the limit of density in the mixed wood seems rather safe.

V. SUMMARY

1. We have studied densities of the spring populations of Great Tit, Blue Tit and Coal Tit (*Parus major*, *P. coeruleus*, and *P. ater*) in two woodland districts in Holland. Both districts contained attractive mixed woods (high densities) and unattractive pinewoods (low densities). Fluctuations from year to year were small in the former and considerable in the latter. As the number of tits increased, density in the mixed wood rose much more slowly than density in the pinewoods. Apparently some mechanism buffers density in the mixed woods.

2. The nature of this buffer mechanism is examined in the Great Tit. Reproduction and mortality can be excluded as possible causes; apparently the mechanism is a component of habitat selection. As a limiting influence of nesting holes, roosting holes and food can be rejected, we assume the following explanation. Great Tits have an aversion for localities which bear a dense population of the same species. The birds seem to prefer mixed woods to pinewoods, but as the mixed woods become more densely populated, excess birds settle in the pinewoods. Thus the attractiveness of the mixed wood per se is counterbalanced by the repelling influence of the population already present. In one case this resulted in the mixed wood being always filled up till a constant level.

3. The limit of tolerable crowding is not the same in all habitats but higher in the more attractive ones. During our observations this limit probably never was reached in the pinewoods.

4. Dispersal of Great Tits over different habitats takes place in autumn and in spring. We conclude that the buffer mechanism works at least in spring. It is unknown whether it acts also in autumn. A partial redistribution of birds during spring must be assumed.

5. Local differences in the census data are discussed. They are most

easily explained by the assumption that the buffer mechanism is the more effective, the greater the difference in attractiveness between rich and poor habitat.

6. Innate standards of tolerable crowding and displacements of individuals seem to be important factors in the regulation of density of Great Tits. Besides the principle discussed in this paper, emigration of young birds in autumn (probably density dependent) much influences the number of birds which settle in a given area (KLUYVER, 1951).

7. Great Tits are territorial birds. In spring the mixed wood is completely divided into territories. Since the density effect works during this season, we assume that it is a consequence of territorial behaviour. A complete proof for this assumption cannot be given, but it seems to us the most reasonable hypothesis.

8. The census data for Blue Tit and Coal Tit agree with the above explanation, but it is not possible to exclude alternative hypotheses.

9. The biological significance of the buffer mechanism in the Great Tit is discussed and some comparisons are made.

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APPENDIX: STATISTICAL ANALYSIS

Prof. L. J. SMID of Groningen University kindly undertook the statistical study of our data. His comments are quoted here.

We consider two neighbouring woods, a mixed wood of O_1 ha and a pinewood of O_2 ha. By way of simplification we suppose that in a certain year n tits (males) of a certain species (Great, Blue or Coal Tit) must settle in the two woods. Then, if the territories have a surface of 1.6 ha in the mixed wood and of 8.0 ha in the pinewood, the numbers of tits are

$$n_1 = \frac{O_1}{1.6} \text{ and } n_2 = \frac{O_2}{8.0}; \quad n_1 + n_2 = n.$$

Now the following "hypothesis of proportionality" can be set up: In any case the tit makes no difference between a certain area of mixed wood and a c (in our case $c = 5$) times larger area of pine wood. Then in other years also, with higher or lower values of n , the proportion of the numbers would be

$$O_1 : \frac{1}{c} O_2.$$

If a diagram is made in the (n_1, n_2) -plane, the points are to be expected on a straight line through the origin (Fig. 3). In reality there are of course many causes for accidental deviations in the ratio c . Thus if n is given, not always the same division in n_1 and n_2 will be obtained, but there is a certain probability distribution on the line $n_1 + n_2 = n$, around the indicated point. If there were no other accidental deviations than those in c , then a higher value of n would correspond to an almost proportionally enlarged distribution. (Exact proportionality is impossible because n_1 and n_2 must have integral values)

On the other hand it may be thought that a tit cannot breed on a territory which is smaller than a certain area of A ha. A rather oversimplified scheme is obtained by supposing that the attractiveness of a territory is measured by the surplus $\frac{O_2}{n_2} - A$ in the pinewood and by $c(\frac{O_1}{n_1} - A)$ in the mixed wood and that in the ideal equilibrium

$$\frac{O_2}{n_2} - A = c(\frac{O_1}{n_1} - A).$$

If $n_1 + n_2 = n$ is variable, this formula represents a part of a hyperbola in the (n_1, n_2) -plane (Fig. 4).

In reality a probability distribution around the regression curve would be obtained. We do not suggest of course that this simple formula really represents the regression curve.

In this case it may be said that density is buffered, in the first place in the mixed wood.

We now will neglect all deviations other than those in c , for example those caused by counting errors and the sampling deviations caused

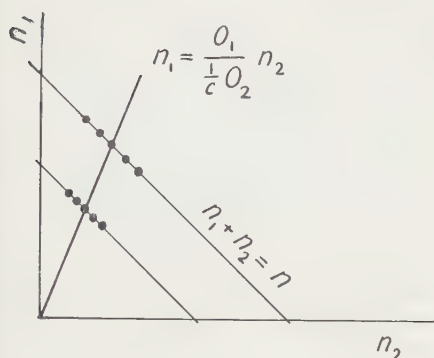


Fig. 3.

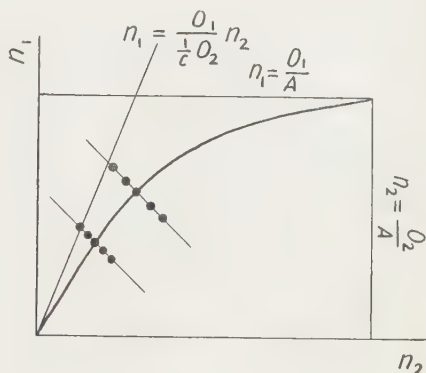


Fig. 4.

by the smallness of the areas of the woods. The correctness of these neglects is questionable.¹ Then if the hypothesis of proportionality holds true the distribution of n_1/n_2 is independent of $n_1 + n_2$. This independency can be checked by testing whether the rankings according to these two quantities are correlated. This may be done by means of Kendall's coefficient of rank correlation² which is ordinarily denoted by τ . As in the alternative hypothesis an increasing value of $n_1 + n_2$ tends to be accompanied by a decreasing value of n_1/n_2 , a one-sided test may be used.

Each of the 5 cases produces a value of τ which is significantly negative, and thus leads to rejection of the hypothesis of proportionality.

Finally, we remark that even the simple fact that in each of the 5 cases τ turns out to be negative provides a significant test against the hypothesis of proportionality.

	Number of years of observation	Probability of obtaining or exceeding the observed value of τ (in case of the hypothesis of proportionality)
Great Tit. Wageningen (1934-1942) .	9	0,0012
Blue Tit. „ (1925-1942) .	17	0,023
Great Tit. Hulshorst (1941-1951) .	9	0,0063
Blue Tit. „ (1941-1951) .	8	0,016
Coal Tit. „ (1941-1951) .	9	0,0063

¹ Moreover, in the Hulshorst data the area of the observed pinewood is not the same every year. We replaced the observations by fictitious observations in a wood of the mean area, by enlarging or reducing the number of tits proportional to the area.

² Cf. M. G. KENDALL (1948) Rank correlation methods. London.

APERÇU SUR LE DÉVELOPPEMENT DE LA THÉORIE DE LA PÊCHE

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INTRODUCTION

La pêcherie destinée à la consommation propre ou locale a coutume de donner chez les peuples autochtones des résultats régulièrement satisfaisants. Par contre, si la pêcherie est exercée comme un métier et qu'on s'efforce continuellement d'augmenter sa production des difficultés se présenteront tôt ou tard.

Anticipant sur les faits à discuter, on peut affirmer que, quand on part d'une pêcherie stationnaire, c.à.d. d'une pêcherie à activité et rendement constants, et qu'à un moment donné on emploie un plus grand nombre d'engins de pêche, on provoquera immédiatement une augmentation de la production. Toutefois, à cause de la décimation du stock de poissons, ce succès sera suivi par une diminution graduelle de la production en poids, jusqu'à ce qu'un nouvel équilibre entre la pêcherie et le stock de poissons soit atteint. Si on a à faire à une exploi-

tation peu intensive, une série d'augmentations soudaines de l'activité aboutira successivement à des équilibres plus productifs jusqu'à ce que les nouveaux équilibres produisent toujours de moins en moins de poisson. Ceci est démontré graphiquement dans la fig. I.

Pratiquement, on n'attend généralement pas d'augmenter le nombre des engins de pêche jusqu'à ce qu'un nouvel équilibre se produise. D'ailleurs les majorations de l'activité des pêches sont plutôt graduelles que soudaines de sorte que l'épuisement des ressources est caché par des succès temporaires. Ainsi il peut arriver qu'on ne se rend compte à temps que l'industrie se dirige vers un point mort.

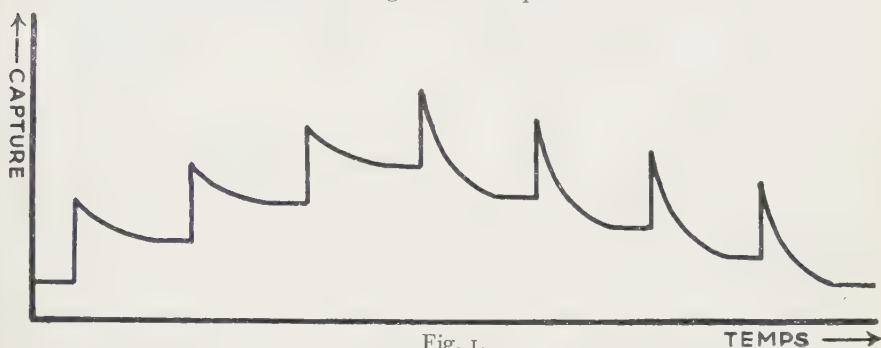


Fig. I.

Ce problème est devenu aigu pour la première fois au sujet de la pêche au chalut en Mer du Nord. Toutefois, dans cette aire l'étude de cette question est fort compliquée étant donné que plusieurs pays exploitent la Mer du Nord avec toutes sortes d'engins et de navires. En outre, à chaque instant, de nouvelles régions de pêche ont été englobées dans la pêcherie. De plus, les améliorations techniques et les fluctuations dans la conjoncture du marché ont ici compliqué davantage les écarts.

Un exemple plus élémentaire nous est donné par M. GRAHAM (1929), traitant la pêcherie du Ngege (*Tilapia esculenta* Graham) dans deux baies (chacune ayant de 30 à 50 milles de largeur) sur les côtes opposées du Lac Victoria en Afrique orientale. Les deux baies sont séparées par un espace d'eau de 200 milles, trop profond pour cette espèce de poisson, tandis que le fond de ces deux baies présentait des conditions vitales analogues.

Dans la première baie, la Baie Kavirondo, on a pêché commercialement avec 250 filets maillants importés (largeur des mailles de 5 pouces), ce qui donna chaque nuit 1.250 poissons, de sorte que chaque filet en captura 5 en moyenne par nuit.

Dans la seconde baie, la Baie Emir Pasha, une tribu de nègres vivant dans cette région ne pêchait que pour sa propre consommation au

moyen d'une sorte de nasse. La pêche ne totalisa pas plus de 100 poissons par nuit. GRAHAM employa ici ses filets maillants et captura avec chacun de ceux-ci en moyenne 27 poissons par nuit. Ces prises correspondaient à peu près avec celles obtenues dans la Baie Kavirondo, quand on avait pêché pour la première fois, en 1914, avec ce genre de filet et lorsqu'on avait recommencé en 1918, après une interruption de quelques années. Les résultats étaient alors d'environ 25 unités par nuit et par filet. On pouvait aisément arrondir à ce chiffre le 27 de la pêche expérimentale.

On peut en conclure, que la densité du stock de poissons dans la Baie Emir Pasha était cinq fois plus grande que celle de la Baie Kavirondo. Les chiffres de la capture par filet et par nuit peuvent être considérés comme étant en proportion avec les densités des deux populations de poissons.

De ce qui précède, on en arrive au tableau suivant :

	Densité du stock	Capture totale par nuit
Baie Kavirondo – pêcherie aux filets maillants .	'5'	1.250
Baie Emir Pasha – pêcherie à la nasse.	'25' (27)	100

Comme la pêcherie avait été stationnaire dans les deux baies pendant un certain nombre d'années, GRAHAM avait des raisons de supposer que les captures habituelles étaient en équilibre avec la production locale de poissons. Les captures futiles de la pêcherie à la nasse étaient donc en équilibre avec la production de la population qui n'était qu'à peine décimée, tandis que la pêche plus active de la Baie Kavirondo était constamment capable de donner des résultats plus rémunérateurs. Remarquablement il paraît que le stock le plus dense était en équilibre avec la plus petite récolte. On pourrait dire que la Baie Emir Pasha souffrait de *sous-exploitation*.

En outre, il est universellement connu, qu'une pêcherie par trop active mène après un laps de temps à un faible profit stationnaire et notamment à des captures de poids réduit comprenant surtout de poissons non adultes, ce qui est caractéristique de *sur-exploitation*.

En combinant cette constatation avec l'expérience de la Baie Emir Pasha, nous arrivons à la conclusion qu'une pêcherie d'intensité moyenne donnera à la longue les meilleurs rendements. Si l'activité de la pêche est telle qu'elle stimule le stock de poissons à la plus grande production possible, alors nous pouvons parler d'une *exploitation rationnelle*.

Si on pourrait disposer de l'expérience de plusieurs équilibres de pêche d'un certain stock, l'intensité d'exploitation qui donne à la longue les meilleurs résultats, se manifesterait d'une manière purement

pratique. Toutefois, une expérience aussi étendue n'est pas ou est à peine réalisable et par conséquent nous sommes amenés à une analyse des modifications que le stock de poissons subit par l'exploitation.

Pour toutes les considérations sur l'exploitation, qui seront données dans les chapitres suivants, chaque espèce de poisson est étudiée séparément. L'espèce en question (ou variété), sa manière de vivre (par exemple: reproduction et migration) ainsi que l'aire (plus ou moins limitée) du stock de poissons sont pour cette étude supposées comme étant connues.

SCHÉMA ÉLÉMENTAIRE NÉGLIGEANT LA MORTALITÉ NATURELLE ET LA CROISSANCE INDIVIDUELLE

Les considérations les plus élémentaires ont été données par W. F. THOMPSON (1937), où il ne tient pas compte de la mortalité naturelle ni de la croissance des poissons.

Comme l'exemple le plus simple, il prend la pisciculture dans un étang. Au début de la première année, on commence, disons, avec 1.000 jeunes poissons. A la fin de la première année, tous les poissons (1.000) sont capturés et remplacés par 1.000 jeunes poissons. L'exploitation commence donc la seconde année de nouveau avec un stock de 1.000 unités. Ceci peut être continué indéfiniment. Si le pisciculteur veut s'abstenir pour une année de vendre et garder le poisson après la première année dans un second étang, il pourra de nouveau vendre chaque année suivante 1.000 poissons, qu'il aura gardé deux ans dans ses étangs; son stock de poissons est alors de 2.000 individus. Si le pisciculteur voudrait s'abstenir de la vente pendant plusieurs années en maintenant son apport régulier de 1.000 jeunes poissons par an, il pourrait, après cette période, faire une récolte annuelle de 1.000 poissons plus âgés et en même temps garder un stock plus grand.

Finalement, il pourrait laisser le premier lot dans l'étang avec les jeunes poissons, et ainsi de suite. Cet exemple, où le poisson plus âgé reste dans le même étang, commence à ressembler aux circonstances, qui se présentent dans une pêcherie. Un exemple numérique nous montre clairement, ce qui se passe quand cette population est soumise à une exploitation constante.

Dans la moitié gauche du tableau ci-dessous, le premier lot qui vient d'être apporté est noté à la première ligne comme 1.000 unités. La ligne suivante montre ce qui arrive au premier lot après une année avec une exploitation de 80%; 200 poissons de ce lot restent dans l'étang et 800 en sont retirés. Les lignes suivantes donnent l'évolution de cette théorie. Avec un rapport d'alevins et avec une exploitation constante, une certaine classe d'âge a la même importance numérique,

qu'avait la classe d'un an plus âgé, il y a un an. La première colonne du tableau est donc l'image de la composition d'âge de la population.

Age	Stock	Exploitation à 80% par an	Stock	Exploitation à 50%, par an
I	1.000	—	1.000	—
II	200	800	500	500
III	40	160	250	250
IV	8	32	125	125
V	2	6	63	63
VI		2	31	31
VII			16	16
VIII			8	8
IX			4	4
X			2	2
XI			1	1
Total	1.250	1.000	2.000	1.000

Ainsi nous voyons que dans la moitié gauche du tableau, avec un apport annuel de 1.000 poissons et avec une capture annuelle de 80 % le stock de poissons s'élève à 1.250 individus et la capture stationnaire à 1.000. De la même manière dans la moitié droite du tableau, nous constatons qu'avec un apport annuel de 1.000 poissons et avec une capture annuelle de 50 %, le stock s'élève à 2.000 poissons et la capture stationnaire à 1.000.

En général, on peut dire, que d'une nouvelle classe d'âge de N individus, une partie p est capturée, de sorte qu'après la saison de pêche, il en reste $(1-p) \cdot N$. La classe d'âge qui a été apportée dans l'étang un an plus tôt a subi le même sort un an plus tôt et au cours de la seconde année une partie p des survivants a été capturée, de sorte que de cette classe, il en reste $(1-p)^2 \cdot N$. A ce moment de la classe d'âge qui est encore d'un an plus âgé, il en restera $(1-p)^3 \cdot N$ etc.

La diminution du nombre d'individus, qu'on trouve dans les différentes classes d'âge, doit donc avec un apport constant, une pêche constante et absente de mortalité naturelle suivre une progression géométrique $(1-p)$. Le stock total S , c.à.d. le nombre total des poissons dans l'étang avant chaque pêche, est alors égal à

$$S = N + (1-p) \cdot N + (1-p)^2 \cdot N + \dots = \frac{N}{p}$$

Il s'ensuit que le stock total est inversement proportionnel à la capture relative p .

En cas stationnaire à p constant, la capture C , c.à.d. le nombre de poissons capturé annuellement, est égal au nombre de l'apport annuel, $C = p \cdot S = N$.

Un tableau numérique nous montre, ce qui arrive avec un apport annuel de 1.000 individus et une capture stationnaire de 50 % (donc d'un stock de 2.000), qui passe soudainement à une capture de 80 %.

Ceci est démontré dans le tableau ci-après.

Classe d'âge	Ans							
	1	2	3	4	5	6	7	8
I.	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
II.	500	500	500	200	200	200	200	200
III.	250	250	250	100	40	40	40	40
IV.	125	125	125	50	20	8	8	8
V.	63	63	63	25	10	4	2	2
VI.	31	31	31	12	5	2	1	
VII.	16	16	16	7	2	1		
VIII.	8	8	8	3	1			
IX.	4	4	4	2				
X.	2	2	2	1				
XI.	1	1	1					
Stock	2.000	2.000	2.000	1.400	1.280	1.256	1.251	1.250
Capture	1.000	1.000	1.000	1.600	1.120	1.024	1.004	1.000
Exploitation. . .	50 %			80 %				

Une exploitation plus intensive provoque donc un succès de courte durée, tandis qu'après quelques années la capture tombe à nouveau au nombre qui doit être équivalent (pour tout équilibre) aux apports annuels du nombre d'alevins (du moins si nous négligeons la mortalité naturelle).

Pour un degré d'exploitation plus grand, le stock a une valeur d'équilibre plus basse, ce qui se reflète dans les faibles moyennes des captures journalières par unité d'engin de pêche.

Si élémentaires que ces exemples puissent paraître, ces principes fondamentaux en deviennent quand-même compréhensibles. Cependant, par suite de sa simplification, cette théorie ne peut pas rendre compte du fait, qu'il y a une intensité de pêche qui peut fournir à la longue un poids maximum de produit. D'ailleurs la croissance des poissons ainsi que leur mortalité naturelle a été négligée dans cet exposé.

LES QUATRE FACTEURS AGISSANT SUR UNE POPULATION EXPLOITÉE

C'est RUSSELL (1931) qui a attiré l'attention sur le fait que le poids d'un stock de poissons est influencé par quatre facteurs (abstraction faite de l'émigration et de l'immigration), à savoir: un accroissement du poids par l'arrivée annuelle de la jeune génération et par la croissance individuelle des poissons; une diminution du poids par la mortalité naturelle et par la capture. RUSSELL en donna l'équation suivante:

$$W_1 = W_0 + R + G - M - F.$$

W_0 = poids d'un stock de poissons à un moment donné.

W_1 = poids de ce stock après un an.

R = accroissement du poids par l'arrivée de la jeune génération.

G = accroissement du poids par la croissance individuelle des poissons.

M = diminution du poids par la mortalité naturelle.

F = diminution du poids par la capture.

A l'état stationnaire, les modifications s'annulent l'une l'autre :

$$R + G = M + F.$$

Examinons maintenant, comment on peut évaluer les quatre valeurs fondamentales : accroissement, croissance, mortalité naturelle et capture.

La valeur la plus facile à obtenir est le poids de la capture. Ceci est donné par la statistique des apports.

Evaluer la mortalité naturelle est beaucoup plus difficile et doit se faire indirectement. En surveillant à quel degré l'importance numérique des classes d'âge décroît, on arrive à l'évaluation de la partie du stock qui disparaît et par la mortalité naturelle et par la capture. D'une autre manière, on obtient la partie qui est capturée et la différence de ces deux résultats donne la partie du stock qui disparaît par la mortalité naturelle seule. Puisque le poids total des captures est connu, on peut aussi calculer la perte de poids causée par la mortalité naturelle.

A cette fin, des échantillons des captures commerciales sont continuellement étudiés au point de vue de la taille, du poids et de l'âge. L'âge est déterminé par la lecture des anneaux d'hiver sur les écailles ou sur les otolithes. Les mensurations établissent le rapport entre l'âge et la longueur (ou le poids). Ce rapport peut être contrôlé par la méthode PETERSEN (1895), par le mouvement des maxima dans la distribution des fréquences de longueur au cours de l'année. S'il s'avère impossible de lire directement l'âge sur les parties dures du poisson, on dépend alors tout à fait de la méthode PETERSEN. Ainsi on peut se former une idée de la composition d'âge des captures.

Avec un apport stationnaire de jeunes classes d'âge et une mortalité stationnaire, la diminution de la fréquence relative des classes d'âge plus âgées dans les captures donnerait la possibilité d'évaluer la partie du stock de poissons qui survit annuellement, donc une évaluation de la mortalité totale, c.à.d. la somme de la mortalité naturelle et de la capture. Il va de soi que, dans ce cas, il faut seulement tenir compte des classes d'âge, dont les individus sont déjà si grands, qu'ils ne peuvent plus s'échapper à travers les mailles du filet. Si on a à faire avec des apports de jeunes poissons forts variables (comme c'est le cas pour le hareng norvégien et pour certaines espèces de Gadidae dans la Mer du Nord), alors il faut surveiller pendant quelques années la décimation d'une (ou de plusieurs) classes d'âges dans les captures commerciales. Ici aussi, il faut seulement envisager les classes d'âge, dont les poissons ne peuvent plus échapper à travers les mailles du filet (JACKSON, 1939).

Afin d'arriver à une évaluation de la proportion du stock qui est capturée annuellement, on applique la méthode de marquage de poissons. Si les poissons marqués se trouvent après un laps de temps dans les captures commerciales, ils sont remis par les pêcheurs contre une récompense. Le nombre de ces recaptures pendant une période déterminée peut nous renseigner quelle partie du stock est capturée durant cette période en supposant que les poissons non marqués sont capturés dans la même proportion que les poissons marqués.

En vertu de ce qui précède, nous savons déjà quelle partie disparaît annuellement par l'ensemble de la mortalité naturelle et de la capture et si les expériences de marquage démontrent quelle partie est capturée, alors la différence entre ces deux proportions donne la partie qui disparaît par la mortalité naturelle seule. En combinant ces nombres proportionnels et le poids total de la capture annuelle, on peut ainsi évaluer le poids des poissons éliminé par la mortalité naturelle, procédé dont nous avons déjà fait allusion ci-dessus.

Le poids total du stock peut être obtenu en combinant la proportion des poissons marqués qui est recapturée et le poids de la capture annuelle totale. En tenant compte de la moyenne du poids individuel, ce résultat peut aussi être exprimé en nombres.

Pour les espèces de poissons ayant des œufs pélagiques, il y a une autre manière pour évaluer la même grandeur. Détermine-t-on par exemple sur un réseau de stations couvrant toute la région de ponte le nombre d'œufs par unité de surface à l'aide d'un filet de plancton verticale, il est possible de calculer le nombre total d'œufs évacués dans la région. Connaît-on le nombre d'œufs qu'une femelle pond en moyenne, on peut calculer le nombre total de femelles qui ont pris part à la ponte et comme ces femelles forment une partie déterminée du stock total de poissons, il est aussi possible de calculer tout le stock. Ceci a été fait pour la première fois par BUCHANAN-WOLLASTON (1926) pour la plie dans la région méridionale et centrale de la Mer du Nord. D'après les deux méthodes on est arrivé à une évaluation de 2 à 300.000.000 d'individus.

En combinant la valeur numérique relative de la plus jeune classe d'âge et le nombre total de poissons du stock, on arrive à évaluer le recrutement.

Le rapport entre l'âge et la longueur (ou le poids) des individus se révèle en mesurant (ou en pesant) des individus de différentes classes d'âge. Au surplus il y a une autre méthode de pouvoir déterminer la croissance individuelle: les expériences du marquage peuvent être utilisées à la résolution de ce problème en mesurant les individus au moment de marquage et ensuite encore une fois lors de la seconde capture. En combinant les données sur la croissance individuelle, la fréquence relative des classes d'âge et le nombre total d'individus, on peut estimer la croissance de la population.

L'évaluation des facteurs dynamiques agissant sur une population exploitée, a donné naissance à une littérature très étendue et un aperçu moderne de ce sujet a été donné par RICKER (1948). Notre exposé assez élémentaire des méthodes ne veut que démontrer que les quatre termes nécessaires pour dresser la balance de RUSSELL deviennent accessibles en principe par des recherches statistiques et biologiques. Toutefois, la dépendance réciproque biologique des quatre quantités R , G , M et F est trop incomplètement exprimée dans l'équation de RUSSELL pour qu'elle puisse expliquer le fait que l'équilibre de la production montre quelque part un maximum pour une certaine intensité d'exploitation.

APPLICATION DU PRINCIPE D'INTÉRÊT COMPOSÉ CONTINU

Au premier développement de la théorie de la pêche on a commencé par caractériser la capture par la partie du stock, qui est capturée annuellement¹. De la même façon les autres principes de gain et de perte étaient déterminés par la fraction du stock, qui était impliqué annuellement dans le mouvement considéré.

Considère-t-on, que tout poids produit en plus d'un stock croissant, participe à son tour à la production, et que toute perte entraîne une

¹ Au cas où le mouvement annuel de gains et de pertes soit grand, ou qu'une période de plus longue durée soit considérée, cette fraction pourrait bien surpasser l'unité.

privation de production, on en arrive à penser à un processus d'intérêt composé.

Pour d'autres raisons aussi, l'ancienne formule donnait lieu à des changements. Un poisson, une fois capturé, ne peut plus après coup subir une mort naturelle. Si l'exploitation est intensive, alors un grand nombre de poissons ne connaîtra pas une mort naturelle. Un poisson, qui, par exemple est capturé en janvier, serait pendant le restant de l'année considéré à tort comme candidat pour une mort naturelle, on sous-estimerait le nombre de poissons pouvant subir une mort naturelle. Il serait plus correct, de clore de temps en temps les calculs et d'en recommencer un nouveau lot. En divisant l'année en un nombre infini de périodes très courtes, la difficulté disparaît totalement.

Par ce qui précède, il est souhaitable de considérer tout le processus comme étant un cas d'intérêt composé continu.

En peu de mots le produit d'un intérêt composé continu donne l'équation suivante.

Si le taux d'intérêt est égal à une partie p ou $100 \cdot p \%$, l'intérêt simple d'un capital K est alors d'un montant pK par an; en ajoutant annuellement l'intérêt au capital K , il est devenu

$K \cdot (1 + p)$ après une année,

$K \cdot (1 + p)^2$ après deux années,

$K \cdot (1 + p)^t$ après t années.

Si les additions d'intérêt se font deux fois par an, le capital s'élève à $K \cdot (1 + \frac{p}{2})^2$ après une année; n fois par an, le capital s'élève après une année à

$$K \cdot (1 + \frac{p}{n})^n = K \cdot \left(1 + \frac{1}{\frac{n}{p}}\right)^{\frac{n}{p}}$$

Pour $n \rightarrow \infty$ ceci devient $K \cdot e^p$. Après t années $K \cdot e^{pt}$. Ceci est valable tant pour les valeurs positives que négatives de p .

L'intensité d'une pêcherie se caractérise par la capture totale pour l'unité de temps. Suivant le choix, ceci s'inscrit en nombre ou en poids. Si l'intensité est variable, il faut la mesurer pendant une très courte période; c.à.d. il faut diviser la capture de cette période très courte par la durée de cette période.

Mathématiquement cela s'écrit comme un quotient différentiel. dN étant le nombre de poissons qui est capturé pendant le temps dt , l'intensité de la pêcherie est donnée par $\frac{dN}{dt}$.

On peut aussi tenir compte du poids de la capture. Si dW est le poids de la capture pendant le temps dt , alors l'intensité de la pêcherie est égale à $\frac{dW}{dt}$.

L'intensité de la pêche peut donc être regardée comme une partie du stock. Quand on procède à évaluer cette partie, on arrive au taux d'intérêt composé continu.

Si on calcule en nombre, on arrive à $\frac{1}{N} \cdot \frac{dN}{dt} = p$, où N est le nombre d'individus du stock.

S'il en va du poids, $\frac{1}{W} \cdot \frac{dW}{dt} = p$, où W est le poids du stock.

Une fois parti à la recherche pour exprimer plus complètement les modifications, que subit un stock exploité, on est arrivé à déterminer l'augmentation ou la diminution du poids par les quatre facteurs mentionnés ci-dessus sous une forme d'intérêt composé. Nous avons alors à faire avec quatre taux d'intérêt r , g , m et f , où les gains et les pertes en poids de RUSSELL en sont respectivement la conséquence.

Ceci s'exprime par: $W_t = W_0 \cdot e^{(r+g-m-f) \cdot t}$.

(BÜCKMANN, 1938).

À l'état d'équilibre, on a $r + g = m + f$ puisque $e^0 = 1$.

Cette équation n'est point encore idéale, par ce que les quatre influences ne se font pas sentir d'une manière également forte pendant les différentes saisons. À ceci, on pourrait remédier en considérant les taux d'intérêt comme des variables périodiques en fonction du temps.

Au lieu de $W_t = W_0 \cdot e^{(r+g-m-f) \cdot t}$
on pourrait écrire $W_t = W_0 \cdot e^{\int (r+g-m-f) \cdot dt}$.

Une difficulté majeure est en outre le r , puisque chez la plupart des poissons l'arrivée de la jeune génération est dans une large mesure (ou mieux dans un grand intervalle) presque indépendante du poids total du stock.

LA PRODUCTION D'UNE POPULATION EN FONCTION DE SA DENSITÉ

Résumons les taux d'intérêt r , g , et m comme étant un taux d'intérêt v de croissance de la population, nous obtenons une grandeur, qui dépend largement de la densité de la population.

Supposons qu'une population (disons par l'une ou l'autre catastrophe) tombe à un niveau très bas; la croissance en poids de cette population serait d'abord minime, par manque de poids participant à la production, soit par croissance, soit par reproduction. Aussi la capacité de production augmentera au fur et à mesure de la reconstitution du stock. Ensuite, on voit que cette capacité de production potentielle ne peut plus se réaliser totalement. Cette limitation de la croissance se fera sentir davantage avec l'augmentation du poids total

du stock, jusqu'à ce que l'accroissement du poids s'arrête complètement, quand le maximum est atteint ce qui est possible dans le milieu déterminé. Donc, pour un poids médiocre la croissance du stock est le plus grand.

Plusieurs auteurs considèrent le taux inconstant v de l'intérêt de croissance naturelle de la population comme proportionnel avec la différence du poids maximum C de la population inexploitée et le poids W de la population à un moment donné.

$$\frac{1}{W} \cdot \left(\frac{dW}{dt} \right)_v = k \cdot (C - W) \text{ ou } \left(\frac{dW}{dt} \right)_v = k \cdot (C - W) \cdot W.$$

où k est une constante (voir GAUSE, 1934).

Cette forme est symétrique à l'égard de $(C - W)$ et de W .

De ceci, il s'ensuit que la croissance atteindra son maximum avec $C = 2W$.

L'idée fondamentale de HJORT c.s. et GRAHAM est celle-ci: s'il y a un certain poids total du stock, où sa croissance est à son maximum, alors par une exploitation stationnaire on pourrait maintenir cette situation favorable, ce qui assurerait à jamais la plus grande production possible.

Cette idée est surprenante par sa simplicité et par sa clarté, mais la mise en pratique se heurte à une difficulté. En effet, la croissance d'une population dans ses différents stades est peu accessible à calculer. D'après les recherches de KLEM (1933) sur les populations de cellules de levure, la croissance serait maximale quand le poids atteint la moitié de sa valeur maximale. Appliquant ces résultats sur les stocks de baleines et des poissons, ceci n'est plus convainquant. L'exactitude de cette supposition a ainsi été le sujet de beaucoup de discussions et VON BERTALANFFY (1934, 1938) était plutôt enclin à admettre une loi pour la croissance individuelle, qui donne une croissance maximale pour un peu moins d'un tiers du poids maximum.

Abstraction faite de cet inconvénient d'ordre pratique, une inexactitude s'abrite dans le raisonnement de HJORT c.s. et de GRAHAM. Une population tenue constante par une exploitation montrera notamment une autre composition d'âge, qu'un stock qui s'accroît sans entraves et qui a atteint le même poids. Si la croissance des poissons n'est pas constante au cours de leur vie, il n'est plus nécessaire que la capacité de production du stock exploité soit égale à celle du stock du même poids, qui se développe librement.

L'ACTION CONTRAIRE DE LA CROISSANCE INDIVIDUELLE ET DE LA MORTALITÉ NATURELLE ET LE STADE CRITIQUE OÙ SE CHANGE LEUR PRÉPONDÉRANCE

Les difficultés précitées peuvent être évitées en partant d'un point de vue tout à fait différent. On peut suivre comment se change le poids

total d'un groupe d'individus, qui à un moment donné commencent leur développement à l'éclosion de l'œuf.

Au cours du temps le poids total du groupe n'est point constant; il est plutôt influencé par deux facteurs, agissant en sens contraire, la croissance individuelle et la mortalité naturelle. Pendant la jeunesse le gain par croissance surpasse la perte par mortalité, de sorte que le poids total s'augmente.

Dans l'âge avancé cependant, la croissance devient de plus en plus faible tandis que la mort augmente, pour frapper à la fin le dernier des survivants, réduisant ainsi le poids du groupe à zéro.

Par suite de ces considérations il est évident que dans un âge intermédiaire, il y a nécessairement un stade critique où le gain s'égale à la perte et le poids total atteint son maximum (HERRINGTON, 1944; voir RICKER, 1945).

Dans la pratique de l'élevage des plantes ou des animaux on dirait qu'à ce stade le produit est mûr et prêt à être cueilli ou abattu. Analogiquement on pourrait dire qu'une pêcherie pourrait rapporter un rendement maximal de poissons en capturant radicalement le groupe au moment où il atteint le stade critique, c.à.d. en pêchant à $j = \infty$ en son temps.

Il va sans dire, qu'une telle pêche exigerait un équipement énorme ce qui la rend irréalisable et injustifiable d'un point de vue économique. Au lieu de s'en tenir à ce précepte à base théorique, il faut donc arriver à un compromis en entretenant une pêche à intensité pratique. Comme il est impossible de tuer tout le groupe au stade critique, il faut se contenter d'en tuer une partie trop tôt et une autre partie trop tard. On pourrait employer des filets dont la largeur des mailles impliquerait les poissons dans la pêcherie bien avant d'atteindre leur stade critique. L'application de cette largeur des mailles donnerait une capture maximale, quand la pêche serait maintenue à une telle intensité, que la somme des pertes par privation de croissance et par excès de mortalité serait restreint au minimum.

Si l'économie impose une restriction plus forte à l'équipement, cela implique l'urgence d'entretenir une intensité de pêche plus faible. Cette intensité faible étant donnée, on peut réduire les pertes au minimum en réduisant la mesure des mailles, et ainsi de suite. Il s'en suit une relation entre l'intensité de la pêche et la mesure recommandable des mailles. Par ces considérations simples et claires, RICKER (1945) a donné l'explication du phénomène de la capture maximum, en même temps reliant la notion de sous- et de sur-exploitation à l'âge lors de la première capture.

L'application de ce principe exige un examen scrupuleux de la croissance et de la mortalité au cours de la vie des poissons. Aussi

RICKER a donné son attention au développement des méthodes convenables à servir à ce but. Enfin la croissance et la mortalité peuvent bien dépendre de la densité de la population, de sorte qu'il faut faire les déterminations dans des circonstances à densités différentes, afin d'éviter une extrapolation dans l'application de sa théorie.

Quel que soit la clarté de cette théorie à grands traits, une complication s'introduit à cause de la variation individuelle de la croissance: l'action sélective des filets s'effectue selon la taille des poissons et point selon leur âge. D'ailleurs, la précision des effets de la privation de croissance et de l'excès de mortalité exige des calculs qui s'étendent à perte de vue. Une tentative plus directe de se rendre compte des résultats des diverses régimes de pêche pourrait être essayée en calculant le poids total des captures, qu'une classe d'âge pourrait fournir pendant les années de son existence.

Cependant, avant de suivre cette voie, nous préférons présenter l'analogie de la pensée de RICKER, en appelant l'attention sur l'assurance d'une reproduction indemne, qu'exige une exploitation stationnaire.

LA DEMANDE QU'IMPOSE LA REPRODUCTION AU RÉGIME DE LA PÊCHE

Tous les régimes de pêche, traités jusqu'ici, donnent à la longue un équilibre à rendement stationnaire quelconque. Il en est autrement, quand la capture est à la fois si précoce et si intensive qu'une génération ne trouve plus l'occasion d'assurer une progéniture capable de reprendre une reproduction au même plan. Un tel régime ne permet aucune stabilisation et l'épuisement devient inévitable.

Chez la plupart des espèces de poissons, la ponte est si abondante et si précoce, que dans un intervalle assez étendu le nombre d'alevins est presque indépendant de la décimation de la population. Toutefois il arrivait que pour l'aiglefin de la Mer du Nord et pour la plie de la Mer Baltique, la production d'œufs resta en dessous du niveau à cause d'une exploitation trop poussée. Pour la période 1918-1930, il s'avérait pour l'aiglefin de la Mer du Nord, que quand une génération jeune de 1.000 alevins aurait l'occasion de produire 34.000.000 œufs, la reproduction serait assurée. BAERENDS (1947) a pris ces faits comme point de départ pour en arriver à des mesures convenables afin d'éviter une décimation de plus en plus désastreuse.

On pourrait prescrire une taille minimum, par laquelle la nouvelle génération ne serait exploitée avant qu'elle ait produit le nombre d'œufs requis et par après capturer radicalement toute la classe d'âge. On pourrait aussi fixer une taille minimum un peu plus petite et alors maintenir l'exploitation à un niveau assez modéré pour que la pro-

duction du nombre d'œufs soit encore justement atteinte. On pourrait fixer également une taille minimum encore plus petite et alors pêcher prudemment, mais à nouveau assez maîtrisé pour que la production du nombre d'œufs nécessaire soit encore atteinte. Chaque mesure minimum correspond donc à un taux maximum tolérable d'intérêt decapture.

Ce raisonnement ressemble beaucoup à celui de RICKER et les relations qui s'en découlent, prennent la même forme; tous les deux donnent des combinaisons d'une taille minimum et d'une intensité de pêche. On pourrait les mettre en diagramme l'un à côté de l'autre. Pour cela on pourrait se servir d'une abscisse indiquant l'intensité de pêche (de $f = 0$ jusqu'à $f = \infty$) et d'une ordonnée indiquant l'âge auquel le poisson atteint la taille moyenne, dont il est question. Ainsi chacune des relations pourrait être représentée par une courbe qui va en montant vers son extrémité d'où $f = \infty$.

Tandis que la courbe de RICKER représente une série de combinaisons recommandées, la courbe de BAERENDS démarque la borne d'une aire fatale; pour toute combinaison de taille minimum et d'intensité de pêche au dessous de la courbe de BAERENDS, le stock s'achemine vers l'épuisement.

Vu que la pratique de la pêche démontre qu'en général ce n'est pas la reproduction qui forme le hic d'une exploitation, la courbe de RICKER doit être située ordinairement au-dessus de celle de BAERENDS. Ainsi, en ce cas, qui est heureusement le plus commun, rien ne s'oppose à se tenir à la courbe de RICKER.

Cependant, pour compléter la théorie, il faut envisager la possibilité où la courbe de RICKER est située (soit en partie, soit en total) au-dessous de celle de BAERENDS. En ce cas ce serait désastreux de se tenir aux recommandations de RICKER. Alors il faudrait recourir au calcul du poids total des captures, qu'une classe d'âge pourrait fournir au cours des années. Ainsi on pourrait s'orienter de nouveau parmi les possibilités de rendement que promettaient les combinaisons du côté sûr, au dessus de la courbe de BAERENDS, pour en choisir la meilleure.

L'ÉVALUATION DU POIDS TOTAL DES CAPTURES FOURNIES PAR UNE CLASSE D'ÂGE AU COURS DE SA VIE OU PAR UNE POPULATION SOUS EXPLOITATION STATIONNAIRE

Les considérations qui ont été données dans les chapitres précédants sur la croissance d'une population en fonction de sa densité, et sur les pertes qu'entraîne la capture graduelle d'une classe d'âge, ont bien aidé à éclaircir quelques aspects de la notion de la capture optimale. Cependant, ces considérations ne se prêtent pas à évaluer des résultats numériques, dont on a besoin pour arriver à la prescription d'un certain régime de pêche. Nous verrons qu'il en est autrement avec la

méthode, où on procède à évaluer le poids total de la capture, que pourrait fournir une population exploitée. Vu que les mérites de toute administration de pêche dépendent du rendement annuel qu'on en peut attendre à la longue, cette voie s'approche le plus directement de la solution de notre problème.

En suivant la décimation d'un groupe d'individus du même âge au cours du temps, on trouve que pendant la première partie de leur vie leur nombre est seulement réduit par la mortalité naturelle; une fois que la génération atteint le stade, qui l'implique dans la pêche, la mortalité par la capture s'y ajoute.

Si les quatre taux d'intérêt sont connus pour tous les stades de la vie des poissons, alors on peut calculer pour chaque époque de l'existence d'une classe d'âge le nombre d'individus décimés, le poids individuel des poissons ainsi que le poids des captures. En additionnant les captures pour toutes les époques, on obtient le poids total des captures que produit cette génération. Pour une exploitation stationnaire ceci est égal à la capture de la population, où toutes les classes d'âge sont à la fois présentes. Pour le calcul du poids des captures stationnaires d'une population, on peut donc suivre les prises d'une classe d'âge depuis le moment où le poisson intervient dans la pêche.

Au point de vue historique, il est intéressant d'apprendre que déjà en 1918 BARANOV a publié un article (en russe), dans lequel il a tenté de trouver une solution par cette voie². Ce n'est que vingt ans plus tard, que le dit article a été traduit en anglais et par là il a été possible d'en prendre connaissance au delà de la Russie. Récemment HOLT et BEVERTON, s'inspirant de l'oeuvre de BARANOV, ont donné au même sujet un développement plus exact et amplifié. Pour cette raison nous nous en tenons à HOLT et BEVERTON dans la suite de notre exposé.

En résumé leur manière de formuler est la suivante: Si N_r représente le nombre d'individus d'une génération au moment où le poisson intervient dans la pêche, \mathcal{W} est le poids de la capture de cette génération au cours d'un certain laps de temps, et ω_t le poids moyen d'un seul poisson au temps t (s'écoulant depuis le moment où la jeune génération commence à être pêchée), alors le poids de la capture de notre groupe étudié dans l'intervalle de temps $t_1 = n$ jusqu'à $t_2 = n + 1$ est égal à

$$\begin{aligned} \mathcal{W} &= \int \frac{d\mathcal{W}}{dt} \cdot dt = \int \left(\frac{dN}{dt} \right)_f \cdot \omega_t \cdot dt = \int N_t \cdot f \cdot \omega_t \cdot dt \\ &= \int N_r \cdot e^{-\int (f+m) \cdot dt} \cdot f \cdot \omega_t \cdot dt \\ &= N_r \cdot f \int_{t_1=n}^{t_2=n+1} \omega_t \cdot e^{-\int (f+m) \cdot dt} \cdot dt \end{aligned}$$

² Voir appendice.

Année par année on calcule le poids de la capture pour en faire finalement l'addition. Si le nombre d'années est λ , nous arrivons à la formule suivante:

$$\sum r_w = N_r \cdot f \cdot \sum_{n=0,1}^{\lambda-1} \int_{t=n}^{n+1} \omega_t \cdot e^{-f(f+m) \cdot dt} \cdot dt$$

D'après cette méthode HOLT et BEVERTON ont pu, tout en calculant, arriver à l'évaluation de la capture totale pour toute une série d'intensités d'exploitation. Comme point de départ, ils choisirent les valeurs qui étaient valables pour la pêcherie de la plie dans la Mer du Nord. De ceci il découlait que, les autres valeurs étant fixées, une pêche plus intensive donne d'abord lieu à un rendement stationnaire qui va en augmentant, et qui atteint assez vite son maximum pour diminuer lentement par après (Fig. II).

En faisant varier une à une les quantités données, ils obtinrent une notion de l'influence qu'exercent les différents facteurs sur l'allure de la courbe, notamment sur la position du maximum.

Tout d'abord, il y a à signaler quel résultat est obtenu en attribuant des différentes valeurs aux facteurs biologiques, c.à.d. à l'importance numérique de la jeune génération, à la croissance individuelle et à la mortalité naturelle.

Quant à la jeune génération, une simple considération nous révèle, que dans l'état stationnaire, le nombre N_r d'alevins n'influence pas la position du maximum. Or, imaginons une courbe pour un N_r de valeur donnée et ajoutons y les captures d'un deuxième groupe tout à fait identique, ceci peut être représenté par un redoublement de la valeur de

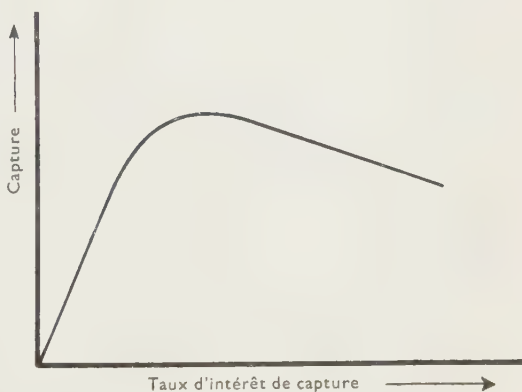


Fig. II.

l'échelle sur l'ordonnée, ce qui démontre clairement que le maximum ne se déplace point sur l'abscisse. La présence de classes riches ou pauvres ne peut donc pas être la cause de sous-exploitation ou de sur-exploitation et ne justifie pas des changements dans l'activité de la pêcherie, si toutefois les autres facteurs (croissance et mortalité naturelle) ne dépendent que très peu de la densité de la population.

Un résultat différent est obtenu en variant la croissance. Une forte croissance fait augmenter le maximum avec une forte régression du

rendement pour une exploitation plus intensive. La capture d'un poisson, quand la croissance est forte, entraîne une grande perte pour la production. Un redoublement annuel du poids individuel donne un sommet bien prononcé. L'équilibre optimum est alors très vulnérable au point de vue de sous-exploitation ou de sur-exploitation et exige de la précision pour sauvegarder cet optimum. Il est à signaler en outre, que dans un intervalle assez étendu pour les changements de croissance, le rendement maximum semble se situer très près du taux d'intérêt de capture 0.25.

Pour une mortalité plus réduite nous constatons le même effet que pour une croissance plus forte; toute la courbe se trouve plus haut et le maximum devient plus prononcé. Pour des valeurs bien différentes de la mortalité naturelle, on trouve que le taux d'intérêt de capture optimum reste de nouveau tout près de 0.25.

Ces explorations arithmétiques sont bien utiles pour se faire une idée sur les possibilités que nous offrent les propriétés naturelles d'une espèce exploitée et la trouvaille que le même taux d'intérêt donne des résultats favorables dans de nombreux cas, est certainement remarquable. L'interdépendance biologique des différents facteurs est cependant négligée au cours de ces calculs.

En premier lieu, il faut envisager une plus forte croissance individuelle dans une population décimée, phénomène qui est connu pour les poissons démersaux. Ainsi une exploitation intense peut favoriser la croissance. En tenant compte de ceci, HOLT et BEVERTON estiment approximativement que le taux d'intérêt de capture optimum provisoire soit de 0.3 à 0.4 au lieu de 0.25 pour la plie dans la Mer du Nord.

Aussi la mortalité naturelle dépendra de la densité de la population; elle diminuera dans une population décimée. Pour la pêcherie de la plie le taux d'intérêt de mortalité naturelle est évalué à 0.05. Il est évident, que ces modifications éventuelles de ce taux n'ont pas de conséquences graves sur le résultat final.

Le développement plus poussé de cette théorie demande des calculs pour une courbe, où il est tenu compte, pour une pêcherie donnée, de la variation des facteurs, qui peuvent être déterminés par la densité réduite de la population, résultant du régime d'une exploitation. Calcule-t-on le rendement pour un certain taux d'intérêt de capture, il faudra donc le combiner avec les autres valeurs qui en dépendent, telles que la croissance et la mortalité naturelle.

Jusqu'ici, cet aperçu mathématique ne concerne que des facteurs qui sont donnés par la nature, ou sont tout au plus influencés secondairement par l'activité humaine. Le facteur qui reste encore à être envisagé, est la taille du poisson, lors de la première capture, caractère qu'on peut régler à son gré par le choix de la largeur de ses mailles.

L'âge appartenant à ce stade varie à son tour dans les calculs (la croissance et la mortalité étant fixées). Il s'en suivait qu'une augmentation de cet âge a pour effet, que le maximum devient d'abord plus grand et se déplace en même temps à droite; enfin un âge plus avancé encore, fait abaisser la courbe du rendement.

Tout ceci s'accorde parfaitement avec la relation de RICKER, concernant la largeur des mailles et le taux optimum de capture. Par suite de cette relation on peut prédire que la courbe que poursuit le maximum du rendement doit nécessairement monter à droite en représentant le plus grand maximum à son extrémité d'où $f' = \infty$; cet extrémité correspond au rendement le plus favorable que pourrait donner une capture soudaine au stade critique de HERRINGTON.

Si une pêcherie ne prenait les poissons que bien après leur stade critique, la courbe du rendement serait abaissée par suite de l'excès de mortalité. La perte pourrait être réduite au minimum par une capture soudaine; il s'en suit que pour les régimes de pêche trop tardives, les courbes du rendement ont tous leur maximum à l'extrémité d'où $f' = \infty$.

Il va sans dire, que pour effectuer des calculs plus achevés, il faut tenir compte de la variation des facteurs biologiques, correspondante à la réduction de la densité de la population, que pourrait entraîner chaque régime de pêche.

Pour chaque intensité de pêche on pourrait alors choisir la taille minimum qui donne la combinaison la plus favorable.

En faisant ce choix, on aurait cependant à veiller de ne pas contrevenir à la demande, qu'impose la reproduction. C'est à ce but qu'un schéma plus compliqué a été déduit, comprenant aussi la production des œufs et la mortalité des œufs et des stades larvaires. La production d'œufs varie à mesure de la population adulte; la mortalité des œufs et des stades larvaires dépend grandement de la densité³. Ces facteurs étant donnés, on peut ainsi évaluer, pour chaque mesure des mailles, l'intensité de pêche au delà de laquelle la population serait épuisée à zéro.

Une autre extension de la théorie pourrait être développée en considérant l'effet d'une exploitation hétérogène où chacun des participants serait libre de choisir à son gré une combinaison convenable d'intensité de pêche et de taille minimum (HOLT et BEVERTON). Une telle extension de la théorie pourrait être utile à servir de base pour arriver à des accords internationaux de pêche.

³ Il en résulte une variation assez affaiblie du nombre d'alevins, ce qui est nécessaire pour arriver à un équilibre stable. Si le nombre d'alevins serait proportionnel à la production d'œufs, la population tendrait à s'accumuler infiniment ou bien à s'épuiser à zéro.

Le présent aperçu se restreint à l'exploitation d'une seule espèce sans s'étendre à l'action réciproque que peuvent exercer entre eux les espèces qui s'entre-dévorent ou se disputent la même nourriture. Bien que ces relations peuvent se changer sous l'influence d'une exploitation, la théorie de la pêche ne s'est guère développée encore sur ce domaine compliqué.

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Je prie M. M. HOLT et BEVERTON (Lowestoft) de trouver ici l'expression de mes meilleurs remerciements pour m'avoir procuré tant d'informations inédites en me prêtant leur manuscrit provisoire en 1948 déjà. En outre je suis reconnaissant au Dr J. HEMELRIJK (Amsterdam) pour ses explications claires et nettes de quelques détails mathématiques.

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APPENDICE

BARANOV a commencé son exposé par donner des considérations sur les équilibres des populations exploitées, telles qu'elles ont été publiées plus amples et plus claires par W. F. THOMPSON en 1937. Ensuite, pour la description de la décimation (par la mortalité naturelle et par la capture), il se servait du principe de l'intérêt composé continu de sorte que les puissances de e entraient dans ses formules.

Du temps de BARANOV on ne disposait pas encore de tant de données sur la relation entre l'âge et la longueur des poissons qu'aujourd'hui. Probablement était-ce pour cela, qu'il s'efforçait de s'exprimer en termes de la longueur l des individus; vu que la croissance ne pouvait être totalement exclue des considérations, il s'accorda à supposer que la longueur croît en progression arithmétique au cours du temps (au moins pendant la période où le poisson contribue ses levées principales à la pêche). En rapport avec ceci, dt prend la place de dl dans ses formules.

Remarquablement il définissait le taux d'intérêt k de mortalité totale comme la mortalité dans l'intervalle de temps, où la longueur des poissons s'accroît par 1 cm. Le nombre de poissons de la population appartenant à l'intervalle $(l; l + dl)$ est alors exprimé par

$$N \cdot dl = N_0 \cdot e^{-kl} \cdot dl.$$

N_0 est, comme BARANOV l'a déjà remarqué, une quantité fictive; si pendant la période succédant à la naissance, la décimation et la crois-

sance montreraient la même constance qui a été acceptée ici pour l'âge plus avancé, alors N_o serait le nombre d'individus de la jeune génération au commencement de leur développement (où l serait égal à zéro). Attendu, que la réalité ne satisfait point à cette demande, aucune interprétation biologique ne peut être attribuée au nombre N_o .

Le nombre d'individus d'une classe d'âge, qui subit ou la mort ou la capture pendant le temps, qu'ils appartiennent à l'intervalle de longueur $(l; l + dl)$ est exprimé par la forme

$$n \cdot dl = n_o \cdot e^{-kl} \cdot dl$$

Ce nombre doit être égal à

$$dN = k \cdot N_o \cdot e^{-kl} \cdot dl$$

de sorte que $n_o = k \cdot N_o$

Si L est la longueur minimum des poissons capturés, alors le nombre total des poissons plus grands que contient la population, est exprimé d'après BARANOV par

$$N_p = \int_L^{\infty} N_o \cdot e^{-kl} \cdot dl = \frac{N_o \cdot e^{-kL}}{k}$$

En suite le poids d'un poisson est mis sous la forme $\alpha \cdot l^3$ (où α est un facteur constant). Alors le poids total des poissons à longueur égale ou supérieure à L , que contient la population, est donné par

$$W_p = \int_L^{\infty} \alpha \cdot N_o \cdot e^{-kl} \cdot l^3 \cdot dl = \alpha \cdot N_o \cdot \int_L^{\infty} e^{-kl} \cdot l^3 \cdot dl.$$

Une application répétée d'une intégration partielle peut réduire cette forme à

$$W_p = \alpha \cdot N_o \cdot \frac{L^3 \cdot e^{-kL}}{k} \cdot \left(1 + \frac{3}{kL} + \frac{6}{(kL)^2} + \frac{6}{(kL)^3}\right)$$

ce qui peut être mis sous la forme de

$$W_p = \alpha \cdot L^3 \cdot \frac{N_o \cdot e^{-kL}}{k} \cdot q = \alpha \cdot L^3 \cdot N_p \cdot q$$

$$\text{où } q = 1 + \frac{3}{kL} + \frac{6}{(kL)^2} + \frac{6}{(kL)^3}.$$

Or, $\alpha \cdot L^3 \cdot q = \frac{W_p}{N_p}$ est égal au poids moyen des poissons capturés.

Cette relation a fourni à BARANOV un point d'application de sa théorie à la pratique de la pêche de la plie dans la Mer du Nord et le Kattegat. C'est qu'il disposait d'informations sur le poids moyen des

plies pêchées. Dans les années 1880, lorsque la pêche était encore insignifiante, et la mortalité totale était presque uniquement due à la mortalité naturelle, le poids moyen s'élevait à 1250 gr. Par cette voie, il tentait d'estimer la mortalité naturelle.

Nous rappelant la relation $n_o = k \cdot N_o$ nous pouvons dire que le poids W_p doit être multiplié avec k pour arriver à la perte totale en poids de la population.

Les taux d'intérêt de capture et de mortalité naturelle soient désignés respectivement par k_f et k_m ; alors la perte en poids mentionnée ci-dessus (résultant de l'ensemble de la mortalité et de la pêche) ne doit qu'être multiplié par $\frac{k_f}{k_f + k_m}$ pour arriver au poids total de la capture annuelle.

Donc, r_w est proportionnel à $q \cdot \frac{k_f}{k_f + k_m}$, les facteurs $a \cdot L^3$ et $N_o \cdot e^{-kL}$ ($= N_r$) étant considérés comme indépendants de l'intensité de la pêche; k_m est connu par estimation.

C'est par cette voie, que BARANOV a calculé le poids de la capture pour des différentes intensités de la pêche. Il lui paraissait que pour une certaine intensité, le rendement atteint son maximum. Cependant, la position exacte du maximum reste discutable par cause de la supposition faite d'un accroissement régulier au cours du temps. Vu que les poissons âgés croissent de moins en moins, cette erreur se fera sentir davantage quand la pêche est peu intensive (et le stock contient un assez grand nombre d'individus âgés,) ce qui influence la situation du maximum.

Une fois, qu'on dispose d'une foule de données sur la croissance des poissons, le détour parcouru par BARANOV n'est plus à la page.

SUMMARY

Practical experience has shown that a sudden increase in fishing effort will cause an immediate rise in catch, which is followed by a downward trend, mostly leading to a balanced situation. Starting from an undeveloped state of fishery, we can arrive at a more profitable balance by augmenting our efforts. Due to this effort the fish population automatically thins out. As soon as we reach a stage, in which more activity would yield less profit in the long run, we are at the verge of over-fishing (Fig. 1).

In order to arrive at an understanding of facts, several theoretical viewpoints have been brought forth in the course of time. This review only deals with the dynamics of one single species under exploitation.

Interspecific competition and predation as influenced by fishing are not considered here.

By a simplified representation of facts W. F. THOMPSON has clarified that intensified fishing efforts will decrease the stock and that sudden increase of efforts will immediately be followed by a bigger catch. Furthermore it is self evident, that the yield in number will in the long run be equal to the recruitment, when natural mortality and migration are negligible.

The different increases and decreases in weight of the stock have been specified by RUSSELL as recruitment, growth, natural mortality and catch. Migration is hereby neglected. It is shown in brief, how we can arrive at an estimate of these factors. With a stationary situation, $\text{recruitment} + \text{growth} = \text{natural mortality} + \text{catch}$. The mutual biological relations of these quantities are not, however, satisfactorily expressed by RUSSELL's balance. Due to this incompleteness of his theory, there is no sound explanation as to why there should be some fishing rate yielding an optimum catch.

The fact that all gains in weight of stock once produced will in turn take part in the production, and that all losses will cause a lack of production, suggests a process of compound interest. The simultaneous cooperation of several changes is most suitably specified as a case of continuous compound interest.

An explanation of the optimum catch has been given by HJORT c.s. and GRAHAM by combining the above mentioned principles, and considering the combined compound interest of recruitment, growth, natural mortality and catch. The total rate of population growth, resulting from these happenings can, however, only be realized in part, depending on the density of the population. When the population is going to restore itself from a very low level after a catastrophe, the total weight of the population will at first increase quicker and quicker, until the increase has reached its maximum. From this stage on, the increase will slow down and come to a standstill when the weight of the population has grown to its maximum. If the growing population was kept on a certain level by continuously cropping off the growth, the maximum stationary yield is supposed to be obtained by keeping the population at the stage of its maximum growth. However, conceivable as it may be, this theory is not fully exact, because a cropped stock will differ from a freely growing population in its age distribution, and hence their producing capacity need not necessarily be the same in a state of equal density.

Another trend of thought has been followed by RICKER, comparing the rates of growth and of mortality of the fish throughout their life history. For some time growth will exceed death, raising the total

weight of the year class. Sooner or later, natural mortality will exceed growth and the bulk of the year class will decrease until finally the last survivor dies. In the intermediate stage, where the rates of growth and of natural mortality are equal, the weight of the year class must attain its maximum (HERRINGTON). So, a sudden kill of the whole year class at this so called critical stage would give the greatest possible yield. An earlier catch will cause a loss by privation of growth; a delayed catch a loss by excess of mortality. In the sea a sudden catch is impracticable; it would require an enormous fishing fleet. As a compromise a fishing activity of feasible intensity should set in prior to the critical stage, in such a way that losses will amount to a minimum. The slighter the fishing activity, the earlier it should start and this would require a smaller mesh size (RICKER). However, the elaboration of a concise survey of possibilities is marred by complex evaluations of losses. Moreover, a complication is imported by individual variation in growth, since nets act according to size and not to age.

A similar reasoning has been given by BAERENDS with regard to reproduction. In order to ensure proper recruitment every generation should be allowed to produce a sufficient number of eggs. If the age at first capture were such that every generation had the opportunity to satisfy this demand before being involved in the fishery, the entire lot could be killed at once without damaging recruitment. In case fishing is started at an earlier date a moderate fishing could still allow sufficient spawning. When started earlier, the fishing rate should be lower. In this way the catchable size of the fish (as determined by mesh size), is again linked to a corresponding allowable maximum rate of fishing. Whereas RICKER's reasoning leads to recommendable combinations, BAERENDS' indicates fishery conditions which keep the stock at the verge of extinction. Practice seems to show that recruitment is not the main bottle-neck of exploitation. However, in case it might turn out to be, primary attention should be given to the demand imposed by reproduction.

A more direct approach to the problem of fishery management can be made by computing the total weight of the yield, supplied by a single year class in the course of years (being equal to the annual yield of a population under stationary exploitation). An early attempt in this direction has been undertaken by BARANOV. Recently a more exact treatment has been developed by HOLT and BEVERTON. For values of growth, natural mortality and age at first capture as applicable to the North Sea plaice fishery, they found that a maximum yield would be obtained when fishing at an inst. rate of 0.25

The yield is proportional to recruitment, but the optimum fishing rate is not affected by fluctuations in the size of the recruit broods.

This factor cannot therefore in itself cause overfishing or underfishing, as long as the other factors remain constant. Growth and natural mortality will, within a wide range of variation, only slightly affect the optimum rate of fishing.

Every rate of fishing will bring about another density of stock, which in its turn may give rise to altered growth and natural mortality. Considering that individual growth may increase in a thinned population (as is the case with plaice in the North Sea), the optimum fishing rate is roughly estimated at 0.3 to 0.4. For an exact evaluation of the yield for various values attributed to the fishing rate, corresponding rates of growth and natural mortality should be taken into account.

An increase of age at first capture (mesh size) increases the maximum, which at the same time moves to higher rates of fishing. An age is eventually reached, when no further increase in the maximum takes place, and it will even fall again. This agrees perfectly well with RICKER's considerations.

For any intensity of fishing a suitable mesh size can be chosen, allowing for the density dependence of growth (and natural mortality); proper attention should be given to the needs of reproduction.

To this end, a more complex population model has been deduced, which includes egg production and mortality of the younger stages as well. For a given mesh size, a value of the fishing rate can thus be determined, beyond which the population would be depleted to zero.

An extension of the theory to the effect of heterogeneous fishing might serve as a basis for international agreements, leaving the participating countries free to choose their own convenient combination of mesh size and fishing activity.

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SPATFALL AND TRANSPORT OF CARDIUM EDULE L.

by

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I. INTRODUCTION

For some years it has been a subject of investigation at the Zoological Station, Den Helder, to determine the distribution and growth of cockles in the Waddensea in order to obtain an insight into the factors controlling them. These investigations have shown that the cockles in this region are limited to flats which emerge at low tide, and that the animals are not distributed at random over these flats, but rather in a way which will be described below.

KREGER (1940) assumed that this unequal distribution was mainly due to unequal spatfall. He made most of his observations on flats near the Zoological Station, where, according to him, more spat fell on the lower than on the higher parts. He assumed that the highest parts received little spat because the water would have given off the latter to the lower parts covered earlier. Also the smaller head of water and the shorter time of submersion over the higher parts would cause a smaller spatfall. According to KREGER these factors, considered to-

gether, would account for the large amounts of spat he found on the lower parts of the flats.

It was remarkable, however, that the largest numbers of adult cockles found by KREGER on the Zuidwal-flats were present on the higher parts and not on the lower ones. This phenomenon also held for two other areas studied by him, and he attempted to explain this by assuming that on the lower parts spat would disappear in larger quantities, so that, ultimately, more cockles would remain on the higher parts. All other areas examined by KREGER showed the smallest numbers of adult cockles on the higher parts, an observation which was well in agreement with his view.

The weak point in KREGER's investigations was that the youngest cockles found by him measured 1-2 mm, these being the smallest specimens retained by his sieve. It has long been known that the larvae of *Cardium* disappear from the plankton at a size of about 300 μ (THORSON, 1946). Therefore, the possibility cannot be excluded that the animals, during the period necessary for growth from 300 to 1,000 or 2,000 μ , were carried to the area in question from other places. In that case, the place where KREGER found his youngest cockles need not necessarily be the place where the spat settled immediately after metamorphosis.

The purpose of my investigation, therefore, was to separate the *direct spatfall* after metamorphosis from the settling of somewhat older spat, which had been transported for some time. This objective was not fully realized, since, owing to practical difficulties, I, too, did not succeed in obtaining the youngest spat. But the importance of transport of older spat by the current was shown with great certainty, and this transport forms the chief subject of my paper.

My investigations (which were carried out in 1950) not only formed the continuation of KREGER's studies in the years 1937, '38 and '39, but also of work carried out by the Zoological Station in the period of 1947-'50. The latter investigations started after the severe winter of '46-'47, when most cockles in the Waddensea died from exposure. The fine, warm weather of the summer of 1947 favoured the development of a new population, and in the autumn of that year the whole area abounded in animals of one single yearclass. It then seemed worth while to follow the growth and density changes of these animals during the following years. This was done by taking samples along a number of traverses. The purpose of my observations was, at the same time, to determine the spatfall along one of these traverses, where the life-history of an older population was known.

The traverse chosen was one which crossed a flat in the middle of the Waddensea, known as Zeehondenplaat (seal shoal) (fig. I). It is

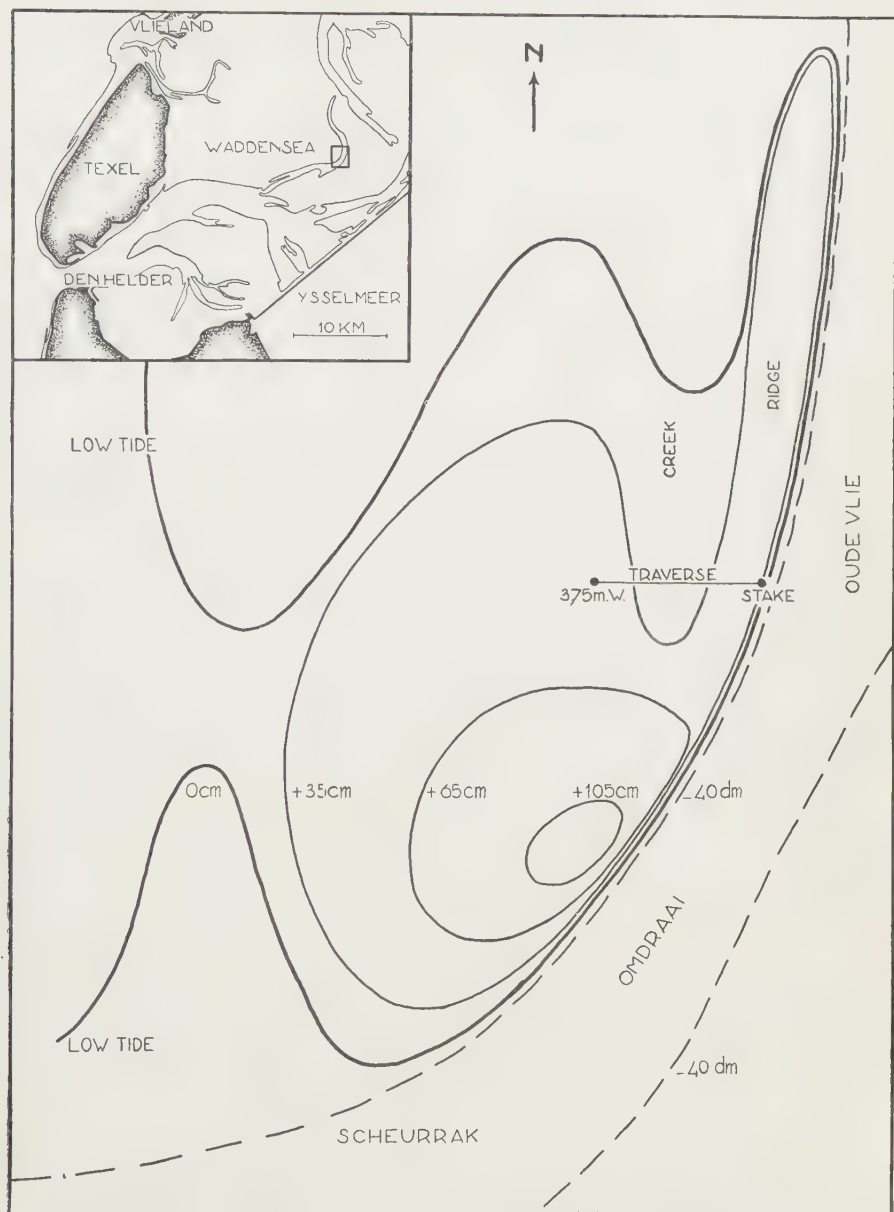


Fig. I. Map of Zeehondenplaat with contour lines and traverse (survey H. Postma, June 7, 1950). The zero-contour represents about mean low tide mark. Inset: Western part of Dutch Waddensea with Zeehondenplaat.

bounded by fairways named "Scheurrak", "Omdraai" and "Oude Vlie". On the highest part of the flat, near the "Omdraai", a group of seals usually had their resting place close to deep water.

Because the present investigations formed part of a larger, more extended research program, I was often able to take advantage of the help and experience of others. In this connection I wish to express my gratitude to Dr J. VERWEY, who suggested the subject to me and critically revised this paper, to I. KRISTENSEN and H. POSTMA for their valuable advice and constant help, and to N. PIJL and A. DRAL for much technical assistance. I owe many thanks especially to miss Marg. HUGHES, London, for her help in the translation of the paper.

II. METHODS

As was already mentioned in the Introduction, we hoped to be able to separate the direct spatfall of newly metamorphosed animals from the settling of older spat, which might have been carried to the spot from other places. To this end, small plots of 20 dm² were made devoid of cockles and re-examined every few days. The occurrence of animals of 300 μ would be an indication of true spatfall, whereas the occurrence of older cockles would indicate that transport of older spat took place.

Apart from this, the spat population of equal plots, which had not previously been cleared of spat, was studied, in order to obtain an impression – from the comparison of cleared and untouched units – of the tenacity of spat at a certain place.

This scheme only partially succeeded. First, it was impossible to make a quantitative investigation of the plots without using a sieve. This sieve had to have meshes not smaller than 0.5 mm in diameter, because otherwise too much sand would be held back. Even by using a 0.5 mm sieve considerable trouble was occasionally experienced when detritus, in the form of fragments of peat, failed to pass through the mesh. Enormous quantities of this detritus were often present in some places, so that the examination of a single sample frequently took several hours. It resulted from the observations that only animals of 600 μ and larger were quantitatively retained by the mesh, whereas animals of less than 400 μ were not retained at all. For this reason, direct spatfall could not be separated from the settling of animals which had been transported a certain time after metamorphosis.

In the second place, it was often impossible to examine the plots at short intervals, of e.g. 1–2 days. Such a regular inspection had originally been planned, because it was realized that animals of say 300 μ might rapidly reach a size of 500 μ and then would be indistinguishable from animals of 500 μ transported to the plot in question.

Subsequently, it was discovered that the growth rate of the youngest spat was much less than originally expected. Moreover, animals smaller than 600 μ were seldom found. For that reason the second draw-back – inspection at longer intervals – scarcely hampered the interpretation of the data. The only disadvantage was that a plot, controlled after e.g. 10 days, was populated almost as densely as the untouched plots.

In the third place, the study of plots not previously examined was later on neglected through lack of time, with the result that only a few data for comparison of cleared and untouched plots were finally available.

For a good understanding of the following work, the methods used must be described in some detail.

A number of plots of 20 dm² along the traverse in question were marked with small poles at their corners. There were 7 of them in all, which are referred to by giving their distance in metres west of a stake placed 40 m from the low tide mark along the "Oude Vlie".

The superficial layer of sand on these plots was removed to the extent of about 2 cm in depth, and sieved. The number of young spat was determined and their length measured. For the shovelling up of the sand a small shovel with 3 turned up sides was used. The latter prevented the water, always present on the sand, from being washed away from the shovel, possibly taking some spat with it at the same time. The residue of the sieved sand was carefully washed over into a glass jar, the contents of which were searched for spat with a 2–3 times magnifying glass. Not only spat of *Cardium*, but also of other bivalves present, were counted, identified and measured under the microscope. Since dead animals can hardly be distinguished from empty shells it was necessary to examine the samples while the animals were still living.

The use of regularly checked plots mentioned above met with some practical difficulties. As a result of the scooping the plots eventually lay somewhat lower than their immediate environment, even in spite of the effort to replace the sand. To some degree the poles, too, were a nuisance by disturbing the regular surface of the sand. Thus it was possible for spat from the surroundings to be washed into these lower lying parts.

Some further experiments were carried out to overcome this difficulty. First, in several places a surface of 2.5 \times 2.5 m was cleared of spat by scooping away the superficial layer of sand (a control of this area showed the absence of further spat). In the centre of these cleared patches a small plot of 20 dm² was staked out, in order to ensure that spat could not be washed into the latter from the immediate surround-

ings. These plots will later be referred to as "isolated plots". The sampling of these plots took place after 12-24 hours.

Another experiment was carried out with pieces of jute (60 × 90 cm), which were spread out and pinned down on the sand. After 12-24 hours the material deposited on these pieces was sieved and examined.

Furthermore, observations were made on the influence of a current shadow on the settling of young spat. To this end screens of iron gauze were placed on the flat at a considerable distance from each other, in directions east-west and north-south. The screens were 1.5 m in length and 30 cm in height. On each side of the screen plots of 20 dm² were staked out, plus one equal plot lying at some distance from each screen for comparison. These areas, too, were sampled after 12-24 hours. In addition, a larger screen was used, which was made of branches. This screen was 3 m long and 30 cm high. Here, too, control areas as mentioned above were used.

On two different days adult cockles were collected along the traverse on plots which had never before been examined. They were counted and the greatest diameter of each annual growth ring, as well as their greatest length, were measured.

Finally, the Zoological Station carried out grain size determinations of the sand as well as current measurements. Grain sizes were determined after VAN VEEN's method (1936), and the figures have been expressed as "median sizes" (KRUMBEIN in TRASK, 1939). Current measurements were carried out by timing the passing of floating algae. The heights of the flat were determined in relation to a certain water level.

III. OBSERVATIONS AND EXPERIMENTS

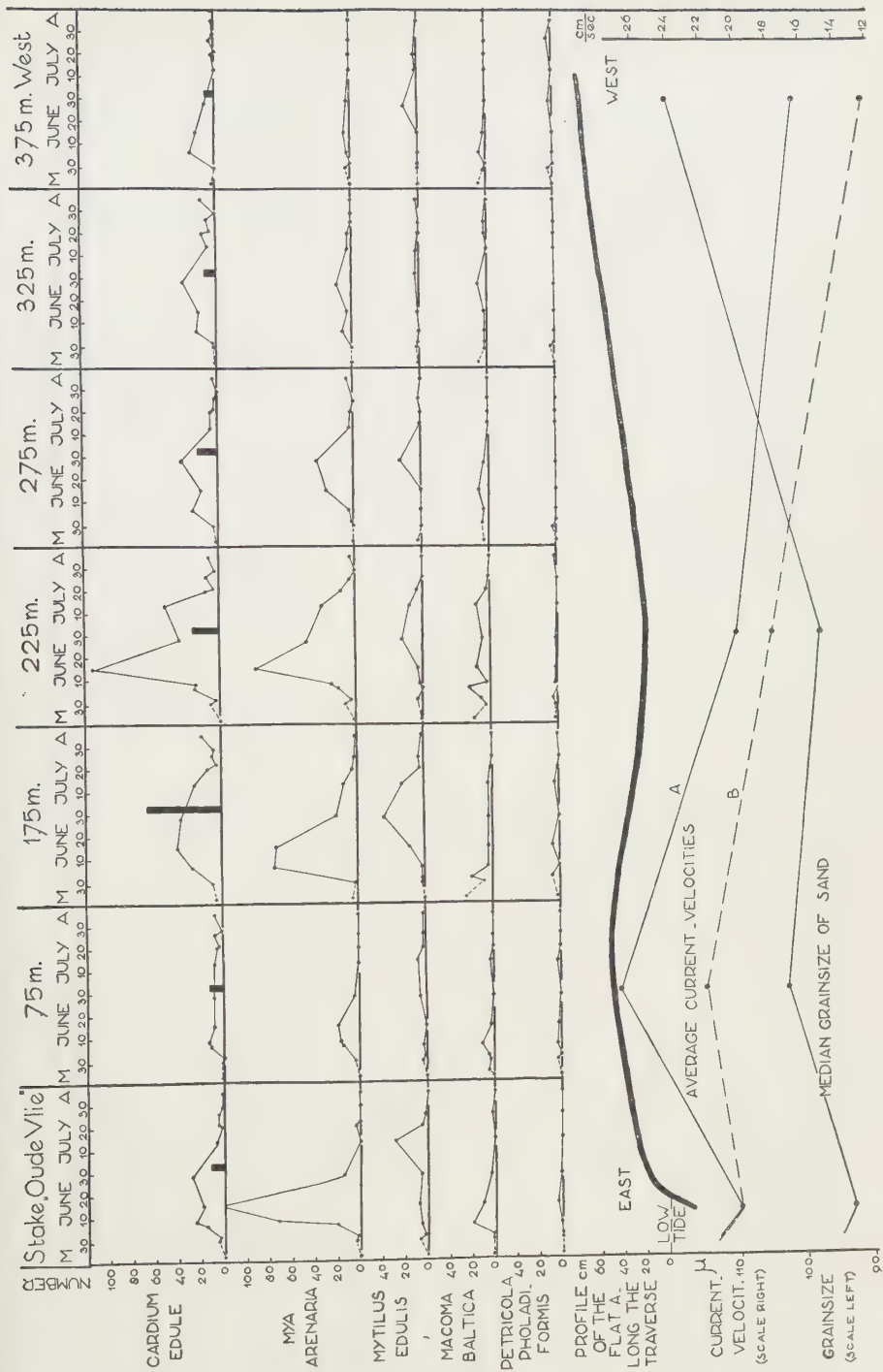
I. TRANSPORT

The data on the occurrence of young bivalves on plots which had been initially cleared are represented in figure II and table I.

In figure II the situation of the plots relative to the stake near the "Oude Vlie" is inserted on top of the columns. The number of animals found is plotted vertically and the different days of sampling are plotted

Fig. II. Numbers of bivalve spat on different plots along traverse in the course of summer. Below: profile along the traverse, average current velocities on June 7, 1950, and median grain size of sand.

Black columns in *Cardium*-curves denote the quantities of 2 and 3 years old cockles. Average current velocities (mean of average flood and ebb velocities, regardless of direction) relate partly (curve A) to periods of submersion alone, periods of emersion having not been taken into account, partly (curve B) to the complete tidal cycle (periods of emersion included).



horizontally in each column. These days were May 24 and 31; June 1, 6, 8, 15, and 28; July 13, 20, 21, 25, 26, 27, and 28, and August 4. The data pertain to spat of *Cardium edule*, *Mya arenaria*, *Mytilus edulis*, *Macoma baltica*, and *Petricola pholadiformis*.

Table I gives the data of *Cardium* in more detail. Here, not only the number of animals is given, but also their size in microns (we will refer to the *italics* later).

TABLE I

Numbers and sizes of *Cardium* spat found on different days on investigation and comparison plots. For explanation see text. Numbers for comparison plots are given in *italics*.

MAY 24	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400- 600	—	—	3	—	—	—	1	4
600- 800	—	1	2	—	1	—	1	5
800-1000	—	—	—	—	1	1	—	2
1000-1200	—	—	—	—	—	—	—	0
1200-1400	—	—	—	—	—	—	—	0
1400-1600	—	—	—	—	—	—	—	0
total	0	1	5	0	2	1	2	11

MAY 31

400- 600	2	1	5	4	1	—	—	13
600- 800	2	—	3	3	1	2	—	11
800-1000	1	—	—	—	2	—	—	3
1000-1200	—	—	—	1	—	—	—	1
1200-1400	—	—	—	—	—	—	—	0
1400-1600	—	—	—	—	—	—	—	0
total	5	1	8	8	4	2	0	28

JUNE 1

400- 600	1	1	—	1	2	1	2	—	1	—	2	7
600- 800	2	3	—	—	7	2	5	2	—	—	4	17
800-1000	1	1	—	4	—	1	—	1	1	1	2	8
1000-1200	—	—	—	—	—	—	1	—	—	—	0	1
1200-1400	—	—	—	—	—	—	—	1	1	—	0	2
1400-1600	—	—	—	—	—	—	—	—	—	—	0	0
total	4	5	0	5	9	4	8	4	3	1	8	35

JUNE 6

400- 600	—	—	7	2	2	1	2	13
600- 800	4	4	8	10	6	7	10	49
800-1000	10	6	9	8	10	7	8	58
1000-1200	1	1	2	1	1	2	1	9
1200-1400	—	—	—	1	3	—	—	4
1400-1600	—	—	—	—	—	—	—	0
1600-1800	1	—	—	—	—	—	—	1
1800-2000	—	—	—	—	—	—	—	0
2000-2200	—	—	—	—	—	—	—	0
total	16	11	26	22	22	17	21	135

JUNE 8	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400- 600	—	2		1				3
600- 800	11	6		8				25
800-1000	8	5		10				23
1200-1400	6	—		2				8
1400-1600	—	—		—				0
1600-1800	—	—		—				0
1800-2000	—	—		—				0
2000-2200	—	—		—				0
total	25	13		21				59

JUNE 15								
400- 600	—	1	1	7	—	—	—	9
600- 800	2	1	1	21	2	1	1	29
800-1000	10	4	16	52	3	5	3	93
1000-1200	3	1	11	9	3	3	—	30
1200-1400	2	—	5	9	4	2	1	23
1400-1600	1	—	4	10	—	—	3	18
1600-1800	—	—	—	2	—	—	3	5
1800-2000	1	1	1	2	2	3	3	13
2000-2200	—	—	—	—	1	1	2	4
total	19	8	39	112	15	15	16	224

JUNE 28								
400- 600	2	1	3	2	1	5	—	14
600- 800	2	—	5	1	3	2	1	14
800-1000	5	2	12	3	6	2	1	31
1000-1200	4	—	3	2	1	—	—	10
1200-1400	2	1	5	5	7	7	1	28
1400-1600	7	2	2	7	7	7	1	33
1600-1800	2	—	—	2	1	4	1	10
1800-2000	2	1	1	4	2	1	1	12
2000-2200	1	1	4	7	3	—	2	18
2200-2400	—	—	1	1	1	—	1	4
2500	1	—	—	—	—	—	—	1
3000	—	—	—	1	—	1	—	2
5000	—	—	—	—	—	—	—	0
7000	—	—	—	—	—	—	—	0
total	28	8	36	35	32	29	9	177

JULY 13															
400- 600	—	—	—	—	3	—	—	—	1	<i>I</i>	—	—	—	4	<i>I</i>
600- 800	2	—	1	—	6	2	9	<i>I</i>	1	—	—	4	—	19	7
800-1000	4	—	2	2	8	3	12	3	3	<i>I</i>	2	—	—	31	<i>10</i>
1000-1200	—	—	1	<i>I</i>	5	2	17	4	1	<i>I</i>	2	2	—	26	<i>10</i>
1200-1400	1	<i>I</i>	2	<i>I</i>	1	—	5	<i>I</i>	—	—	1	<i>I</i>	—	10	5
1400-1600	—	—	1	2	1	—	5	<i>I</i>	—	—	1	2	—	8	5
1600-1800	—	—	—	—	—	<i>I</i>	—	<i>I</i>	—	—	—	—	—	1	0
1800-2000	—	—	—	—	—	—	—	<i>I</i>	—	<i>I</i>	1	—	—	1	2
2000-2200	—	—	—	<i>I</i>	—	—	—	<i>I</i>	—	—	—	<i>I</i>	—	0	3
2200-2400	—	—	—	—	—	—	—	—	—	—	2	—	—	1	0
2500	—	—	—	—	—	—	—	—	—	—	—	<i>I</i>	—	0	1
3000	—	—	—	—	—	—	—	—	—	—	—	<i>I</i>	—	0	1
5000	—	—	—	—	—	—	—	—	—	—	—	—	—	<i>I</i>	0
7000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
total	7	<i>I</i>	7	7	24	8	48	<i>14</i>	6	3	7	<i>14</i>	0	6	99

JULY 20	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400- 600	2	1	1	1	1	2	--	8
600- 800	—	—	1	1	—	4	--	6
800-1000	1	—	2	3	2	4	--	12
1000-1200	—	2	2	3	1	1	--	9
1200-1400	—	—	2	1	1	—	1	5
1400-1600	—	1	2	1	—	1	—	5
1600-1800	—	—	—	1	—	—	—	1
1800-2000	—	—	—	1	—	—	—	1
2000-2200	—	—	—	—	—	—	—	0
2200-2400	—	1	—	—	—	—	—	1
2500	—	—	—	—	—	—	—	0
3000	—	—	2	—	—	—	—	2
5000	—	—	—	—	—	—	1	1
7000	—	—	—	—	1	—	—	1
total	3	5	12	12	6	12	2	52

JULY 21

400- 600	2	—	1	1	1	—	—	5
600- 800	1	1	—	1	—	2	—	5
800-1000	—	1	—	1	2	2	—	6
1000-1200	1	1	1	2	—	1	—	6
1200-1400	—	—	—	—	—	—	—	0
1400-1600	—	—	1	—	—	—	—	1
1600-1800	1	—	—	—	—	—	—	1
1800-2000	—	—	1	—	1	—	—	2
2000-2200	—	—	—	—	—	—	—	0
2200-2400	—	—	—	—	—	—	—	0
2500	—	—	—	—	—	—	—	0
4500	—	—	—	—	—	—	—	0
6500	—	—	—	—	—	—	—	0
6900	—	—	—	—	—	—	—	0
8900	—	—	—	—	—	—	—	0
total	5	3	4	5	4	5	0	26

JULY 25

400- 600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
600- 800	1	1	2	2	3	—	—	4	1	—	1	—	—	—	—	8	7
800-1000	3	1	2	2	2	4	5	4	1	1	4	2	2	—	19	14	
1000-1200	—	1	2	—	2	1	1	5	—	2	1	—	2	2	8	11	
1200-1400	—	—	—	2	1	—	1	—	—	—	—	—	—	—	2	2	
1400-1600	1	—	—	—	—	—	2	2	—	—	—	1	—	—	3	3	
1600-1800	—	—	—	—	—	—	1	—	—	1	—	—	—	—	1	1	
1800-2000	—	—	1	—	—	1	1	—	—	—	—	—	—	—	2	1	
2000-2200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	
2200-2400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	
2500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	
4500	—	1	—	—	—	1	—	—	—	—	—	—	—	—	0	2	
6500	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	
6900	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—	
8900	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	
total	5	5	7	6	8	7	11	15	2	4	6	4	4	2	43	41	

JULY 26	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400- 600	— —	— —	— —	— —	— —	— —	— —	0 0
600- 800	2	—	—	— 1	1 1	—	— 1	1 5
800-1000	2 1	3 2	— 1	1 3	3 2	3 3	1 1	13 13
1000-1200	— —	2 —	— —	1 4	1 1	— 1	— —	4 6
1200-1400	— —	3 1	— —	2 —	1 —	— 1	— —	6 2
1400-1600	— —	— —	— —	— —	1 1	1 —	— —	2 1
1600-1800	— —	— —	— —	— —	— —	— 1	— 1	0 2
1800-2000	— —	— —	— —	— —	— —	— —	2 —	0 2
2000-2200	— —	— —	— —	— —	— —	— —	— —	0 0
2200-2400	— 1	— —	— 1	— —	— —	— 1	— —	0 3
2500	— —	— —	— —	— —	— —	— —	— —	0 0
4500	— —	— —	— —	— —	— —	— —	— —	0 0
6500	— —	— —	— —	— —	— —	— —	— —	0 0
6900	— —	— —	— —	— —	— 1	— —	— —	0 1
8900	— —	— —	— —	— —	— —	— —	— 1	0 1
total	2 4	8 3	0 3	4 8	7 5	4 7	1 6	26 36

JULY 27

400- 600	— —	— —	— —	— —	— —	— —	— —	0 0
600- 800	— 1	1 —	— —	— 2	— —	— 1	— 1	1 5
800-1000	1 2	1 3	3 —	4 1	2 1	1 3	1 1	13 11
1000-1200	— —	— —	— —	3 1	2 —	— —	— —	5 1
1200-1400	— —	1 —	— 1	— —	— 1	— 1	— —	1 3
1400-1600	— 1	— —	1 —	— 1	— —	— —	— —	1 2
1600 1800	— —	— 2	— —	1 —	— —	1 1	— —	2 3
1800-2000	— —	— —	1 1	— —	— 1	— 1	— —	1 3
2400	— —	— —	— —	— —	— —	— —	— —	0 0
3000	— —	— —	— —	— 1	— 1	— 1	— —	0 3
3300	— —	— —	— —	— 1	— —	— —	— —	0 1
4200	— —	— —	— —	— 1	— —	— —	— —	0 1
5400	— —	— —	— 1	— —	— —	— —	— —	0 1
6500	— —	— —	— —	— 1	— —	— —	— —	0 1
7000	— —	— —	— —	— —	— —	— —	— —	0 1
9600	— —	— —	— —	— —	— —	— —	— 1	0 1
11000	— —	— —	— —	— —	— —	— —	— —	0 0
total	1 4	3 5	5 3	8 9	4 4	2 8	1 3	24 36

JULY 28

400- 600	1 —	— 1	— —	— —	— —	— —	— 1	1 2
600- 800	1 1	— 3	1 3	— 1	— —	— 2	— —	2 11
800-1000	— —	1 1	5 2	— 3	— 3	— 1	1 —	7 10
1000-1200	— —	— 1	— 3	1 —	— —	— —	— —	1 4
1200-1400	— —	— —	1 —	2 —	— —	— —	— —	3 0
1400-1600	— —	— —	— 4	1 —	— —	— —	— —	1 4
1600-1800	— 1	— —	— —	— —	— —	— —	— —	0 1
1800-2000	— —	— —	— 1	— 1	— 1	— —	— —	0 3
2400	— —	— —	— —	— —	— —	— —	— —	0 0
3000	— —	— —	— —	— —	— —	— —	— —	0 0
3300	— —	— —	— —	— —	— —	— —	— —	0 0
4200	— —	— —	— —	— —	— —	— —	— —	0 0
5400	— —	— —	— —	— —	— —	— —	— —	0 0
6500	— —	— —	— —	— —	— —	— —	— —	0 0
7000	— —	— —	— —	— —	— —	— —	— —	0 0
9600	— —	— —	— —	— —	— —	— —	— —	0 0
11000	— —	— —	— —	— —	— —	— —	— —	0 0
total	2 2	1 5	7 14	4 5	0 4	0 3	1 2	15 35

AUGUST 4	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400-600	— —	— —	— —	— 1	— —	1 —	— —	1 1
600-800	— —	1 2	4 2	4 12	2 3	6 2	— —	17 21
800-1000	1 —	2 4	6 9	2 5	2 4	4 4	2 3	19 29
1000-1200	— —	1 1	4 2	3 3	— —	— 1	— —	8 7
1200-1400	— —	3 —	1 3	— 1	— —	1 —	— 1	5 5
1400-1600	1 —	— 1	2 —	— —	— 1	1 1	— —	4 3
1600-1800	— —	— 1	— 1	— 4	— —	— —	— 1	0 7
1800-2000	— —	— —	— 2	— 1	— 1	— —	— —	0 4
2400	— —	— —	— —	— 1	— —	— —	— —	0 1
3000	— —	— —	— —	— —	— —	— —	— —	0 0
3300	— —	— —	— —	— —	— —	— —	— —	0 0
4200	— —	— —	— —	— —	— —	— —	— —	0 0
5400	— —	— —	— —	— —	— —	— —	— —	0 0
6500	— —	— —	— —	— —	— —	— —	— —	0 0
7000	— —	— —	— —	1 —	— —	— —	— —	1 0
9600	— —	— —	— —	— —	— —	— —	— —	0 0
11000	— —	— —	— —	— —	— —	— —	— 1	0 1
total	2 0	7 9	17 19	9 29	4 9	13 8	2 6	54 80

From these data it follows that especially in June large numbers of spat settled on the cleared plots. The number and size of *Cardium* spat found after inspections *within 2 days* are given in table II (this table has been derived from table I, the data of all plots having been taken together).

TABLE II

Date	Total number of <i>Cardium</i>	400-600 μ	600-800 μ	800-1000 μ	1000-1200 μ	1200-1400 μ	1400-2000 μ
31-5 — 1-6 . . .	8	2	4	2	—	—	—
6-6 — 8-6 . .	59	3	25	23	8	—	—
25-7 — 26-7 . .	26	—	1	13	4	6	2
26-7 — 27-7 . .	24	—	1	13	5	1	4
27-7 — 28-7 . .	15	1	2	7	1	3	1
Total	111	6	33	58	18	10	7

From the distribution of cockle spat over the different size classes it appears that spat smaller than 600 μ were rarely found; these specimens are likely to have passed through the meshes of the sieve. But it is quite obvious that transport of spat larger than 600 μ took place regularly and that animals larger than 1,000-2,000 μ were also transported.

This conclusion is confirmed by data obtained from the sampling of the so called "isolated plots" (see p. 320). Such plots were made near the "Oude Vlie" and along the traverse at 225 and 375 m west of this point. The results are given in figure IIIa and among others in table IIIa. In figure IIIa both number (vertically) and size (horizontally)



Fig. IIIa. Numbers and sizes of spat settled on isolated plots (for explanation see text). The figures 8, 14, and 20 below the bivalve names denote sizes of 800, 1400, and 2000 μ .

Fig. IIIb. Numbers and sizes of spat settled on jute (60 \times 90 cm) (for explanation see text). Sizes of spat as in fig. IIIa.

[illegible]

TABLE IIIb

Total numbers of spat of different sizes found on all cleared and comparison plots examined.

Total of spat found on :	400- 600 μ	600- 800 μ	800- 1000 μ	1000 -1200 μ	1200 -1400 μ	1400 -1600 μ	1600 -1800 μ	1800 -2000 μ	2000 -4000 μ	4000 -8000 μ	9600 μ	11000 μ	Number of plots examined
Cleared plots	25	108	107	40	22	13	10	2	—	—	—	—	69
Compar. plots	10	59	71	23	13	13	13	14	10	5	2	1	41

are given for 3 species of bivalves, viz. *Cardium edule*, *Mytilus edulis* and *Petricola pholadiformis*.

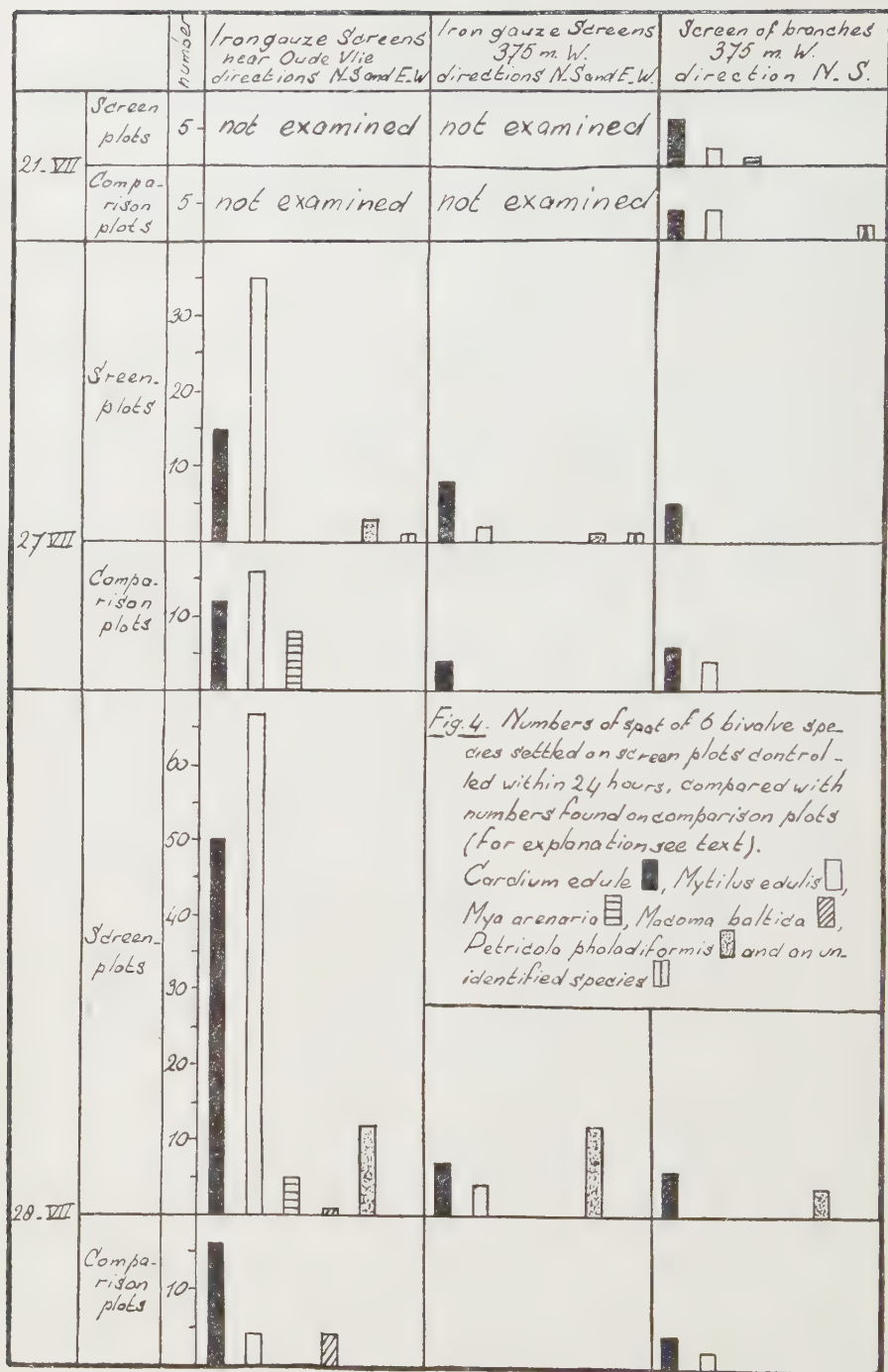
From this it is clear that sometimes after only 12 hours relatively large numbers of animals had settled down on these plots. Their size varied from 400 to 800 μ .

A similar result was obtained for the spat on the pieces of jute (figure IIIb and table IIIa). The jute had been spread out near the "Oude Vlie" and at distances 225 and 375 m to the west. Again, it is obvious that within a short time (12-24 hours) large numbers of spat had settled down on this substratum. The quantities found here cannot be compared with those on other plots (jute 54 dm² and normal plot 20 dm²). Besides, jute as substratum cannot be compared with sand, as its hairy surface may retain the spat. However, this experiment was not made to reproduce normal conditions, but to show that transport takes place, and it is clear that this transport is, biologically, important.

Eventually, transport of young animals was shown to occur by means of experiments in which screens were used (see p. 320). These screens were placed near the "Oude Vlie" and at a point 375 m to the west (figure IV and table IIIa). In fig. IV the numbers of spat of 5 species of bivalves are represented. Samples were taken on the screen plots (on both sides of the screens) and on plots of the same size some distance away from the screens (so that the plots were not influenced by the latter), both being sampled within 24 hours. The size of spat found on the screen plots is given in table IIIa.

From these data it appears again that transport of young bivalves took place regularly and that *Cardium* was transported up to a size of 1,600 μ . At the same time it follows from these figures that usually more spat are found on the screen plots than on the comparison plots. This is caused by the current shadow near the screens, which enables the spat to accumulate there.

It is apparent from all data mentioned so far that transport of young spat must be considerable.



2. TRANSPORT AND SIZE

All observations have shown that young *Cardium* spat, up to a long time after metamorphosis, are being transported by the current. Now, it is worth while to know at what size the young animals are no longer transported. It was possible to decide this by comparing the sizes of animals found on the regularly cleared plots (so called "transport plots") and those found on places never cleared before ("Comparison plots"), where the young spat had time to grow after settling. Such comparison plots were examined along the traverse (table I, *italics*) on June 1 and on July 26, 27, and 28; near the screens they were examined on July 21, 27, and 28 (figure IV).

In table IIIa the number and size of spat found on transport plots cleared within 24 hours are given, together with the number and size of the animals found on the comparison plots. The data of the transport plots are obtained from plots along the traverse, near the screens, and from the isolated plots and pieces of jute. The figures in the last column indicate the number of plots of 20 dm² inspected at the different places.

In table IIIb the numbers and sizes of all animals found on the transport plots are compared with those of the spat present on the comparison plots. The figures in the last column indicate that a total of 69 transport plots and 41 comparison plots were examined.

In the first place, it appears that on the comparison plots, where the population was able to accumulate up to the day of sampling, we seldom found more spat than on the transport plots. Apparently, large numbers of spat disappear regularly from both transport and comparison plots. This disappearance will have been caused partly by mortality and partly by transportation to places elsewhere. The important rôle of mortality is shown by the decrease in numbers in the course of the season (figure V). Although more spat is being reproduced regularly, the quantity does not increase. In previous years it has also been evident that mortality has a great influence on the *Cardium* population (KREGER, 1940, data Zoological Station, unpublished). During one single day, however, only a few animals will disappear as a consequence of mortality, so that the great disappearance of spat during that time must have been caused mainly in another way: there is a constant supply and removal of spat.

The extent of this transport can be expressed by a certain measure, the rate of transport. We can specify this rate as the ratio of the number of animals found within a certain time on a transport plot to that found within the same time on a comparison plot. Both plots will contain about the same number of newly settled spat and the surplus on the comparison plots may be considered as a remnant of the population,

which had settled previously. It should be realized that the rate of transport found will probably be too low, because each individual may have been replaced several times by another one.

On calculating the rate of transport from the figures of table I one obtains for an area of 20 dm² rates of 0.72 (July 26), 0.66 (July 27), 0.43 (July 28), and 0.68 (August 4).

In the second place, it follows from the figures of table III a and III b, that the largest cockles on the transport plots measured 1,600–1,800 μ . On the whole, only 2 animals of 1,800–2,000 μ were found on these plots. On the comparison plots, however, the largest animals were 3,000–9,000 μ . This difference is so striking, that one cannot but conclude that on the “Zeehondenplaat” young cockles up to 1,800–2,000 μ are transported regularly by the current and that cockles are only able to settle permanently when larger than about 2,000 μ .

Unfortunately, during the months of investigation, the numbers of young *Mya*, *Macoma* and *Petricola* in our samples were so small that they could not be treated in the same way as the numbers of *Cardium*. *Mya* was sometimes found (on transport plots) measuring 2500 μ . *Macoma* was never found larger than 3,000 μ , and *Petricola* never larger than 1,200 μ . The number of *Mytilus* was comparable with that of *Cardium*. Animals larger than 1,800 μ were very seldom found and they were present in equal numbers on both transport and comparison plots. This indicates that in *Mytilus*, too, transport by the current must be considerable. It further seems to suggest that these animals do not settle permanently on the flats, for we never found animals larger than 2,000 μ attached to sandgrains.

The question now arises as to why *Cardium* on the “Zeehondenplaat” is no longer transported by the current on reaching sizes of 1,800 μ and larger. There are two possible answers to this question:

1. The current running over the flats might be too weak to transport animals larger than 1,800 μ .
2. Animals larger than 1,800 μ might be unaffected by the current, because they are capable of burrowing deeply into the sand.

1. With regard to the first possibility an attempt was made to test the hypothesis by comparing the rates of sinking of young cockles and of sandgrains in seawater. Once the maximum grain size of the sand transported by a certain current over the flat is known, it becomes deducible at what size young cockles can still be transported by the current.

On July 20, a day without wind, N. PIJL determined the quantity of sand transported by the current 40 cm above the bottom during both ebb and flood. The quantities varied from 0.3 to 5.1 gr per litre. The median grain size of this sand was 1,00 μ , while a large number of grains of 200 μ and even 250 μ were found in ebb and flood samples.

The rate of sinking of live, young *Cardium* was determined after the method described by GRAY (1941). The determination was carried out

at a temperature of 20–23°C, and the results are given in table IV.

There is no close relationship between the sinking rates of cockle spat and sand, and this will have to be ascribed to the behaviour of the animals on falling. They may have their shells open as well as closed and this will have a great influence on their sinking rate.

In spite of the relatively poor correlation, it still follows from the figures that 40 cm above the bottom animals of about 800 μ (corresponding with sandgrains of about 100 μ) can easily be transported, and as numerous grains of 200–250 μ were also found, it is likely that cockles of 1,100–1,600 μ may have been transported at this level. Close to the bottom animals of this size will most certainly have been transported. They can be compared in size with relatively coarse sand.

TABLE IV
Sizes of *Cardium* and sandgrains with the same sinking rates

Temp.	Median size of <i>Cardium</i>	Median size of sandgrains
20° C	2000 μ	320 μ
20° C	1900 μ	215 μ
20° C	1600 μ	230 μ
23° C	1140 μ	253 μ
23° C	1110 μ	145 μ
23° C	760 μ	94 μ
23° C	720 μ	60 μ

The result of this experiment is in full agreement with that obtained from table IVa and IVb, viz., that on the “Zeehondenplaat” the current is able to transport *Cardium* spat up to a size of 1,800–2,000 μ .

2. No observations were made with regard to the question whether or not young cockles of a certain size can burrow so deeply into the sand that they are no longer removed by the current. However, very young cockles will almost certainly be washed out. They will always be able to burrow during periods when the water is still, but when the current increases the uppermost sandlayer will be stirred up and very small cockles will be easily washed away.

The same does not hold for adult cockles, which are far more deeply embedded and thus will not be carried off, except, perhaps, in very strong currents or in areas greatly influenced by wind. Without further investigation it is impossible to give a critical current velocity, at which cockles of a certain size can no longer be washed out and transported, but the fact that so many young cockles up to a size of 1,800–2,000 μ are regularly being transported indicates that animals of this size can be removed by the current.

3. TRANSPORT, CURRENT VELOCITY, AND PLACE OF SETTLING

As already mentioned in the Introduction, KREGER supposed the presence of large amounts of cockles in certain places to be caused by 3 factors. The highest parts of the flats would receive little spat because the latter would have remained behind on the lower parts, covered earlier. Moreover, the smaller head of water and the shorter time of submersion over the higher parts would cause a smaller spatfall there. Therefore, the spat would be accumulated on the lower parts of the flats.

In our investigation a great difference in spat population was noticed when comparing the shallow creek (175–225 m west of the “Oude Vlie”) with the higher parts of the flat (375 m west). Figure II represents the relative height of the flat along the traverse and also gives the median grainsize of the sand at each of the places examined. It can be seen from this figure – and also from fig. I – that there is a low ridge along the “Oude Vlie” and a shallow creek (being hardly more than a subsidence) behind it. The slope of the creek is steeper east than west. Further westward the flat slopes upwards gradually. The grainsize of the sand is coarser on the ridge than near the “Oude Vlie” or in the creek. Still further west the sand becomes even coarser.

It follows from figure II that the largest amount of spat transported was found in the above mentioned creek and along the border of the “Oude Vlie”, whereas the smallest quantities occurred on the ridge and on the highest part. The same holds, in principle, for all other species of bivalves investigated. *Mya* shows a distinct decrease in quantity to the west and a very pronounced increase in number along the “Oude Vlie”. It seems justified, therefore, to assume that the presence of large quantities of transported spat in the creek and along the border of the “Oude Vlie” represent the usual phenomenon over this flat. Unfortunately, the quantity of *Cardium* spat close to the “Oude Vlie” could not be determined because of the presence of large amounts of detritus, which made analysis of the samples impossible.

In the case of the pieces of jute and the isolated plots (fig. IIIa and IIIb) there are also indications that the largest numbers of spat were found in the creek. This supports the previous hypothesis.

It is necessary to state once again that these data exclusively concern *transported* animals, which had been metamorphosed some time previously. They do not refer to the *direct spatfall* of newly metamorphosed specimens. It is therefore still unknown whether or not the border of the “Oude Vlie” and the creek are the most likely places to receive *direct* spatfall.

On comparing places with the most prolific settling of transported

spat with places of the greatest abundance of adult cockles (born in 1947 and indicated with black columns in figure II), it must be stated that the adult animals are most numerous in the creek and along the "Oude Vlie" (about 30 m west of the stake not indicated in figure II, where their number was 90 on 20 dm²), and that their numbers decrease westward.

The largest quantities of adult cockles are present, however, eastward of the places where the spat are most numerous. The number of adults on the ridge is small and does not increase very much on the outer slope near the stake, where the spat do increase. The adult animals are most numerous at low tide mark of the 'Oude Vlie' (30 m west of the stake), where the quantity of spat could not be determined owing to the presence of much detritus.¹

On considering the results of these experiments it must be concluded that the creek and the border of the "Oude Vlie" were not only favourable for the young cockles in 1947, but also for transported spat in 1950. Conditions for settling, therefore, appear to be very favourable there.

When we try to account for the accumulation of large numbers of animals in certain places, it seems justifiable to look for a relation between the number of animals and the current velocity. It has been observed that frequently animals up to 2,000 μ are transported by the currents, so that current velocities must be of great importance. The rate of sinking of young cockles in comparison with sand grains also supports this belief. Therefore, it was originally thought that the settling of large numbers of transported animals in certain places would directly depend on the low transporting capacity of the current at those places.

If it is true that the transport of *Cardium* spat may, to a certain extent, be compared with that of sand, it is important to bring the grain-size distribution under consideration. In the drawing up of the following considerations, POSTMA has kindly assisted me.

Current and wind are the two most important factors that stir up the water. The finest sand and mud are found in places where the current is weak and where at the same time the wind gets little hold on the sea bed. Such circumstances are found in quiet places under the lee of land and often at the transition lines between the channels (fairways) and the flats, but not on the flats themselves. There, the

¹ From investigations of the Zoological Station in the years prior to 1950 it is known that in those years the original distribution of young cockles in 1947 was about the same as that found in the present investigation. KRISTENSEN, who carried out the former investigations, supposes that in the winter of 1949-'50 the then two years old animals were carried away towards the east by the very strong west winds. A similar displacement eastward of old animals along other traverses was observed earlier by the Zoological Station.

current is weak enough to deposit fine materials, but the wind has (through the waves) too much grip upon the flat.

From this point of view the grainsize distribution of the sand on and near the "Zeehondenplaat" (figure II) must be considered. On the bottom of the "Oude Vlie" coarse sand is found (median grainsize about $250\ \mu$). This can be understood, because in the "Oude Vlie" strong currents are running. Along the border of the "Oude Vlie" the sand is fine (about $60\ \mu$), but from this place westwards the grain-size increases gradually, except in the creek. This increase goes hand in hand with a decrease in current velocity. It is very likely, however, that the influence of the wind must be held responsible for the greater coarseness of the sand on the higher parts of the flat.

Judging from the current velocities measured it looks as if in the creek a small grainsize is correlated with a greater current velocity. Currents, however, were measured at the surface, and it is probable that in the creek the relationship between surface and bottom currents is not the same as on the flats. During the greater part of the tide the surface water over the creek runs nearly perpendicular to the direction of the latter. Close to the bottom, however, the water may not be able to develop the same velocity as at the surface, because it is caught between the creek slopes. Only when the surrounding area has run dry the water follows the direction of the creek; then, however, currents have become weak. The current, therefore, must have little transporting capacity along the bottom. This supposition also accounts for the presence in the creek of much detritus in the form of small pieces of peat, etc. This material is quite easily transported and can, therefore, only be expected in places where currents are weak. The creek thus forms a kind of accumulation basin for all kinds of easily transportable materials. The presence of large quantities of detritus along the border of the "Oude Vlie" can be explained in the same way.

In view of the preceding discussion it can be understood why such large quantities of young cockles and other bivalves are present in the creek and along the border of the "Oude Vlie". Their presence is caused by the current, which, on losing velocity, drops the young bivalves it has carried from elsewhere. The experiments with the screens also showed that current shadows may cause an accumulation of spat (see p. 329).

There is, however, a second possibility which might explain the presence of large numbers of young cockles in certain places, viz., the *direct spatfall* immediately after metamorphosis. Here we must return to KREGER's point of view. He supposed that more recently metamorphosed spat would fall on places which were deeper than their immediate surroundings (see p. 334). This is still an unproved sup-

position, but it might be true. In that case, the large numbers of spat in the creek and along the "Oude Vlie" would mainly be due to the fact that these animals had settled there directly after metamorphosis. The presence of so much spat on our cleared transport plots could then also be explained by assuming that these specimens were carried in from the immediate surroundings. Following this train of thought the small numbers of spat on the highest parts of the flats might be due to the fact that but few animals fell there immediately after metamorphosis. The transporting capacity of the current, then, would not be the main cause for the presence of much spat in a certain place, but rather the direct spatfall of newly metamorphosed animals. To reach a definite conclusion on this question the distances should be known over which the animals found in the samples of the cleared plots have been transported.

Unfortunately, the data collected during this investigation are not quite sufficient to decide the matter. Possibly, the direct spatfall plays a certain rôle in the distribution of spat over the flats. On the other hand, transportation by the currents has been shown to be of great importance for the ultimate distribution of cockles over the flats.

It would not be correct to conclude from the foregoing that large numbers of cockles can only be expected in fine sand. Several investigators have already pointed out that there is no correlation between the actual grainsize of the sand and the number of cockles present (KREGER, 1940; WOHLBERG, 1937; SMIDT, 1951). They often found large numbers of cockles both in very coarse and very fine sand. This seems to contradict the foregoing, but it must be borne in mind that the grainsize of the sand in the present investigation was only used as a *relative* measure, to indicate places with stronger or weaker currents or places where the wind has more or less influence upon the flats. Sand was used as a measure for the transporting capacity of the currents. It is clear that a correlation between the grainsize of the sand and the numbers of cockles present need not be expected.

In using fine sand as an indication for weak currents or little wind influence it must also be realized that the presence of many cockles might be the cause of an accumulation of fine sand. The animals are producing large quantities of faeces and pseudofaeces, which in the long run will form a layer over the cockles. It is therefore necessary, when using the grainsize of the sand as a measure for the current velocity and wind influence, to take this factor into account.

4. DURATION OF TRANSPORT

An attempt was made to get an insight into the rate of growth of cockles by measuring the maximum size of the animals on different days in the course of the season. For this purpose data from plots which had never been cleared before (comparison plots) were used, because only here could animals be expected, which had been able to grow undisturbed. The data have been separated for the lower and higher parts of the flat, because it was known that the growth rate

of older cockles on these places was different and, this might hold for the young animals also.

At the beginning of the season the individuals are rather uniform in size, and while the smallest animals are regularly being supplied in the course of the season by settling of new young spat, the shifting to the right of the largest sizes in the length-frequency distribution curve gives a possibility for studying growth. The estimations of the rate were carried out on the basis of daily compound interest. Unfortunately, our data are rather limited in this respect.

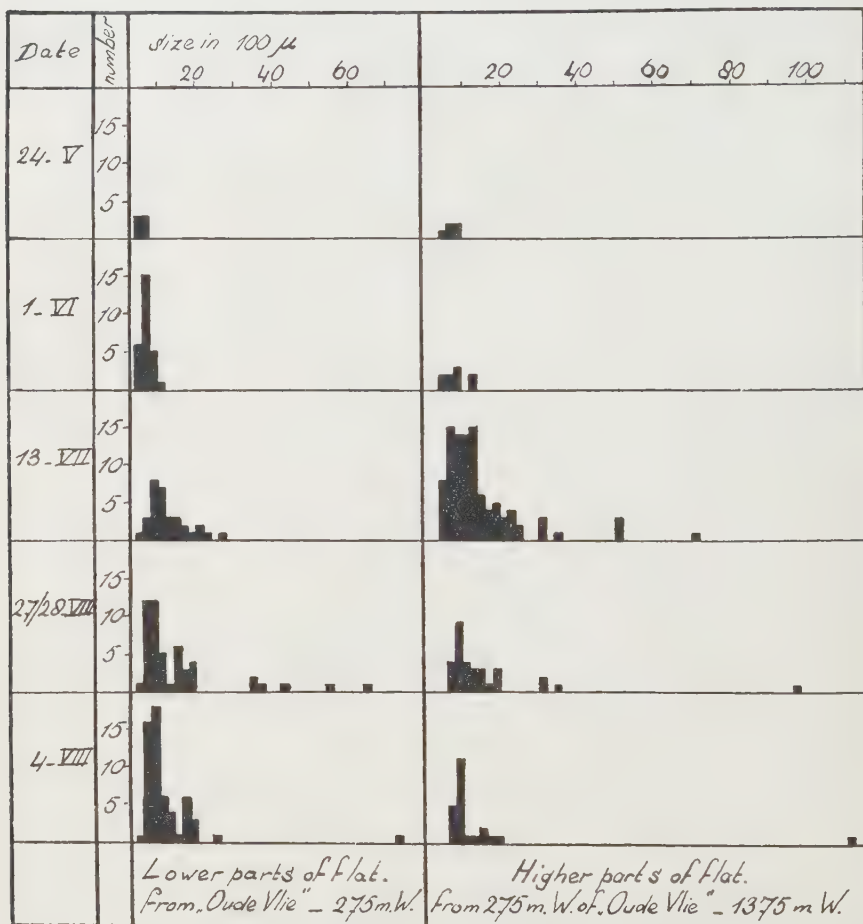


Fig. V. Length frequency distribution of young *Cardium* at different dates on lower and higher parts of the flat. Left: lower parts of the flats between Oude Vlie and 275 m West. Right: higher parts between 275 and 1375 m West. Data refer to plots not previously cleared, compare text.

Later in the season mortality, and also the individual variation in growth, cause the largest animals to be rarely present. The estimation of the rate of growth has, therefore, become less accurate for the older animals (table V and figure V).

These figures show that the young cockles grow fastest on the highest parts of the flat. A similar result was obtained when the annual growth rings and the maximum size of adult cockles were measured. KREGER (1940) has already recorded this phenomenon and given an explanation of it.

TABLE V

Date	Number of days	Lower parts of the flat			Higher parts of the flat		
		Max. size in micr.	Growth in micr.	Growth/day in % of initial size	Max. size in micr.	Growth in micr.	Growth/day in % of initial size
24-5		800			1000		
1-6	8	1200	400	5.2	1400	400	4.3
13-7	43	2600	1400	1.8	7200	5800	4.2
28-7	15	6500	3900	6.3	9600	2400	1.6
4-8	6	7200	700	1.7	11000	1400	2.3

Our data are certainly not sufficient as a reliable source for growth measurements of young cockles of different ages, but they do give an impression of the growth rate. It follows from table V that the length of animals of 300–800 μ most certainly does not increase more than 5 % a day, so that a young cockle of 300 μ must need 10 days to reach a length of 500 μ and at least 20 days to reach 800 μ . SMIDT (1951) gives about the same rate of growth for cockles in the Danish Wadden-sea. In other words, a large part of the young cockle spat is being transported here and there for weeks, before being able to burrow definitely. Certainly, spat of 1800 μ may have been transported for more than one month. Only very quiet places may form an exception to this rule.

5. TIME OF SPATFALL

The graphs of figure VI represent the average numbers of spat of *Cardium* and other species of bivalves for 2 week-periods between May 15 and August 15. The height of the columns gives the average number of spat falling on 1 plot of 20 dm² per day.

It follows from these data that the largest numbers of *Cardium* and *Mya* spat (over 600 μ) were present during the second half of June. Smidt (1951) found the same for *Cardium* in the Danish Waddensea. The largest numbers of *Mytilus* were present from June 15 to July 15,

while *Macoma* showed its maximum shortly before this period. For *Petricola* few data are available, so that nothing reliable can be said in this connection. After the middle of June the quantity of *Mya* spat decreases more rapidly than that of *Cardium*; the quantity of *Mytilus* spat decreases rapidly after the middle of July.

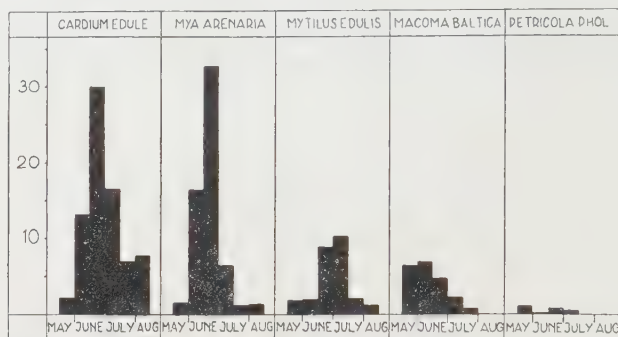


Fig. VI. Average numbers of spat fallen on one plot of 20 dm² per day within periods of 2 weeks between May 15 and August 15, 1950.

Most *Cardium* measured 800–1600 μ during the second half of June. According to previous calculations (see page 339) these animals were at least 20–30 days old, so that the greatest spatfall of newly metamorphosed *Cardium* probably commenced in the second half of May.

On June 2 only a few spat measuring 800 μ were present, and on August 5 much spat still remained. Thus, the first spatfall of *Cardium* must have taken place during the first half of May and the fall was not completed by the second half of June. It is clear that the period of spatfall of *Cardium* in 1950 covered at least 3 months.

IV. CONCLUSIONS

In considering the most important results of this investigation a negative statement must first be made, viz., that it is still unknown as to whether or not newly metamorphosed *Cardium* show any preference for certain places to settle. My attempts to collect the youngest spat were fruitless. KREGER's supposition, that recently metamorphosed animals would come to rest on the lowest parts of the flats, is therefore still unproved.

It could be shown, however, that spat of 600–1800 μ are being transported regularly by the current in large quantities. Strong indications were obtained that these animals, whose rate of fall can be compared with that of sand of 100–250 μ , are deposited especially on places where currents are weak and where winds get little hold on the flat.

In the area investigated this was the case on the lower parts of the flat, which formed an accumulation basin for all kinds of easily transportable material. If KREGER's supposition, that more spat probably fall on the lower than on the higher parts of the flats, would appear to be true, the numbers of such spat would at any rate be much increased by the supply of somewhat older animals from elsewhere by the current. From lack of sufficient data it is, however, impossible to weigh the relative importance of these two phenomena.

It is clear that in the area where the work was carried out the young cockle does not obtain hold directly after metamorphosis (except perhaps in places with a very weak current or with little wind influence), but is being transported for a considerable length of time. Everything points to the fact that the definite settling of spat only takes place when the animals have reached a size of 1000 μ or more. Investigations of SMIDT (1951) appear to show that young cockles are able to settle permanently directly after metamorphosis. It must therefore be assumed that the strong currents in the western Waddensea are the main cause of the long transportation of spat.

V. SUMMARY

Observations and experiments were carried out in the western Waddensea in the summer of 1950 in order to determine the factors governing the settling of spat of *Cardium edule* and other bivalves.

It appeared that young cockles were being transported by the currents for a long time after metamorphosis, until they had reached a size of 1800–2000 μ . It could be calculated from growth rate data that such animals must be at least 4 weeks old.

Strong indications were obtained that most animals are accumulated in quiet places, where currents are not sufficiently strong to carry them away. On the flats investigated these quiet places were characterized by a finer grain size of the sand compared with that of the surroundings and by the accumulation of all kinds of easily transportable material.

Spatfall of *Cardium edule* took place from the first half of May till, at least, the second half of July. The greatest spatfall took place during the end of May.

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ANNUAL REPORT
OF THE ZOOLOGICAL STATION OF THE
NETHERLANDS ZOOLOGICAL SOCIETY
FOR THE YEAR 1952

Our previous annual report¹ held out the prospect of a survey of the Station's activities during the 20 years that have elapsed since its reorganisation. We hope this survey will be accomplished in the course of 1953. A concise review has already been given at the Society's meeting of September 19th–20th, when the Society made an excursion to Den Helder.

During 1952 the spatfall of the mussel again predominated all other items of ecological research. The students working at the Station as well as the Station's personnel spent much of their time on this subject; especially our biological analyst Mr DRAL was almost constantly engaged in this work.

The young mussel spat, which has a size of 250–300 μ at metamorphosis, settles preferably on algae and hydroids, and only after a certain lapse of time does it gradually shift over to the musselbanks. This fact, which was ascertained in foregoing years, was taken as a starting point for our research in 1952. In this connection we were especially interested in the nature of the stimulus on which this curious preference for algae and hydroids may depend. Following several initial trials, threads of different material and different diameters were fastened on wooden frames in the sea, and, in contrast with these, plastic panels with grooves of varying width were also hung out.

¹ The Annual Reports for the period 1876–1928 have been published (in Dutch) in „Tijdschrift van de Nederlandsche Dierkundige Vereeniging” for those years. The Reports for 1952 and onward will appear in “Archives Néerlandaises de Zoologie”. Those covering the intervening years were not published, but a review of the Station's activities during the years 1931–1951 will be given as a separate publication in this journal.

In this way the densities of spatfall on different substrata could be compared well.

The investigations were carried out by Miss GEELEN (Utrecht) and Mr DE BLOK (Leiden). They found that the spat prefer threads to grooves. The threads should be thin and not too smooth. Embroidery silk turned out to be one of the best threads. The numbers of spat per unit of length on silk thread even surpassed those on algae and hydroids. Our former supposition that the more or less plastic properties of hydroids and algae would favour the settling was not confirmed. It seems to be the filiform condition of the material, which is essential. The checking of the test substrata has to be carried out under the microscope and this makes the job time consuming and tedious. The results, however, are well worth the trouble.

Once the use of artificial silk had yielded suitable quantitative data, the influence of such factors as light and current could be included in the scope of the experiments. This possibility was made use of by Mr ROTH (Leiden), who tried to trace the effect of the tidal phase on spatfall, whereas the settling of spat at different depths was studied by Mr DE BLOK, in cooperation with Miss GEELEN. The results seem to fit in with the observations made by Mr LUCAS (Leiden) and Mr ANTHEUNISSE (Utrecht) on the behaviour of the larvae in the plankton, as well as with data on normal spatfall, obtained by Mr LUCAS, Mr DE BLOK, Miss COOL (Leiden) and Miss GEELEN, by the Station's personnel and the students attending the summer courses. In this way the complex picture of a seemingly simple phenomenon as spatfall is being completed step by step. It is hoped that the investigations will be continued by other workers in 1953. The results will be published in this journal.

One of the most striking features revealed by the findings of DE BLOK and GEELEN is the general restlessness of the young animals. The algae and hydroids harbour spat of different sizes up to 1000–1200 μ . This size, however, is not attained in a sessile state. Individual shifting takes place at a rate of some 20% a day. The question arises whether the young of other Lamellibranchs are equally on the move before reaching their final place.

The investigations on the pumping of mussels entered a new phase through the work of Dr TAMMES, who was assisted by Mr DRAL. They inserted a plastic tube in the exhalant siphon of live mussels and then immobilized tube and shells in a plaster cast, letting the inhalant opening free. The discharged water could thus be isolated for analysis when the animals were given different suspensions. The size distribution of the suspended particles was examined in the water on both sides of the mussel. It was found that comparatively coarse material

(30-40 μ) was wholly retained and that finer particles (1-5 μ) largely escaped the mussel's selective action. Except in the case of the coarsest particles, it is possible for the mussel to change its straining rate considerably. These findings did neither tally with the idea that the straining could be brought about by a sieve formed by gill openings, nor by that of a mucus ultra sieve. The suspended particles, either small or large, are supposed to be retained when they contact the cilia of the gills. Large particles should then more likely be hit and retained than smaller ones.

This picture was confirmed by direct observations on very young mussels, where it was possible to look right through the shells. The large latero-frontal cilia were seen sweeping through the water like swaying lime sticks and the adhering particles being wiped off to the row of frontal cilia, from which they were further transported to the food groove.

The pumping output of the so prepared mussels was subnormal, so that the recorded quantities could only be attributed a relative value. Still, the method is excellent to establish the effect of external conditions, e.g. temperature, on the pumping rate. It would be worth while to extend the results already obtained in this direction.

The experiments on the sense physiological relation between Nudi-branchiate slugs and Coelenterates were, for a month, continued by Miss DE KONING (Utrecht). Previously, it had been shown that the slug can find anemones or hydroids against the current. It was then assumed that under the conditions used there was no scent gradient. In order to ascertain that the current actually directs the search of a slug once excited by scent, experiments were devised in which there were currents and no gradient in scent. Unfortunately, these trials had to be discontinued by unforeseen circumstances. It is hoped that the subject will be taken up again in the near future.

An inquiry into the possible influence of light or darkness on the vitality of settled young cockles and mussels was started by Mr BAS from Leiden. No results can as yet be given. It is felt, however, that subsequent experiments should as far as possible be made under natural conditions, since such problems cannot easily be solved indoors.

The study of migrants was carried on as before by buying up southern species offered by local fishermen. In 1952 Mr KRISTENSEN again spent much of his time on this work.

Pre-war observations had suggested that two groups of migrants occur in the North Sea, viz., 1. those which enter in spring or early summer through Dover Strait, and, 2. those which reach us in the autumn after having rounded Scotland. Generally speaking, all species arriving with us in autumn or winter were since that time consider-

ed to have entered the North Sea in the North. Mr KRISTENSEN's data more and more suggest that these species arriving late in the year largely represent animals which flee for cold. There is no sufficient reason, therefore, to assume that all of these animals have rounded Scotland; some of them indeed are hardly known from there. Since the latter are neither observed with us in spring, however, Mr KRISTENSEN supposes that they may enter through Dover Strait, keep to the East-Anglian side, and then hide during summer on stony grounds, where fishing is seldom practised, till they are driven from there by cold. We may expect some more evidence on this point in the years to come.

Part of the southern migrants, recorded in 1952, are enumerated in the list below.

I. The species denoted by numbers 1-8 are supposed to have entered

Species	Size in cm	Locality
I. Southern migrants, supposed to have entered the North Sea through Dover Strait.		
1. <i>Acipenser sturio</i>	± 100	off Texel, near Silverpit-Texel nr 5, 30 m
2. <i>Clupea pilchardus</i>	20-23	8, Texel dike; 64, surroundings Texel Hole
3. <i>Merluccius merluccius</i>	$\delta 57$	off Zuiderhaaks, 18 m
4. <i>Hippocampus europaeus</i>		southern part Dutch coast
5. <i>Spondyliosoma cantharus</i>	22-33	Texel Hole-Oyster Grounds, 29-36 m
6. <i>Box boops</i>	30	Texel dike
7. <i>Atherina presbyter</i>	6-14.4	coastal waters
8. <i>Trigla cuculus</i>	17.5-33	between Silverpit and Dutch coast
II. Tardy southern species, that have possibly entered through Dover Strait.		
9. <i>Petromyzon marinus</i>	75	neighbourhood Texel Hole, 30 m
10. <i>Scylliorhinus catulus</i>	$\varphi 61$; $\delta 59$	neighbourhood of Texel Hole
11. <i>Raia brachyura</i>	60-89	neighbourhood of Texel Hole
12. <i>Raia montagui</i>	30-70	between Silverpit and Dutch coast
13. <i>Solea lascaris</i>	26	N. of Terschelling, 38 m
III. Southern species, supposed to have rounded Scotland.		
14. <i>Cetorhinus maximus</i>	± 25	Den Helder harbour
15. <i>Brama raii</i>	51-60	14, stranded; 6, Texel Hole-Oyster Ground
Northern species, that have reached the southern North Sea from the North.		
16. <i>Gadus virens</i>	41-22	neighbourhood of Texel Hole, 29-32 m
17. <i>Molva molva</i>	46	Texel Hole, 30 m
18. <i>Onos cimbrius</i>	15, 18, 19, 20	Callantsoog-IJmuiden, 7-9 m
19. <i>Raniceps raninus</i>	5.0-5.7	5 from Waddensea, 5 from North Sea, 2-15 m
20. <i>Labrus berggylta</i>	31; 30	Den Helder dike; off Zuiderhaaks, 18 m
21. <i>Crenilabrus melops</i>	$\delta 18$	off IJmuiden, 18 m
22. <i>Anarhichas lupus</i>	36-45	neighbourhood of Texel Hole
23. <i>Scorpaena dactyloptera</i>	15; 17.7	Callantsoog, 9 m; near buoy Silverpit-Texel nr 3, 30 m

the North Sea through Dover Strait. The following notes on them may be added to the data in the list. *Box boops* rarely reaches our coast, only 8 specimens being known to us from there. *Atherina presbyter* may apparently propagate on our coast: about 100 young of 6 cm length were caught leeward of Texel in September. *Trigla cuculus* was less abundant in 1952 than during the period 1946-'50; prior to 1940 it was rare with us.

II. The numbers 9-13 comprise species that may have entered the North Sea through Dover Strait, but were only caught on their way back in winter. Of these, *Scylliorhinus catulus* hardly occurs in the North Sea, 5 specimens being known to us from the Dutch coast up till now; of *Solea lascaris* 10 specimens are now known from the Dutch coast.

Numbers per month										
F	M	A	M	J	J	A	S	O	N	D
	2	¹ 4	60	6 ¹						
			2		⁴ 8	7	2	1		
			¹ 1	¹ 1	¹ 1		± 100			
	2	2	14	3	7	3	3	1		
									¹	
1♀	1♂								2	
2	1								18	5
5	72	15	4	2	4	4		1		¹
								1	9	10
		¹	¹							3
		¹	¹							
	1	2						1		
	5	5								
					¹		¹			
	1									
		4		¹	¹					
				¹		¹				

III. Numbers 14-15 represent southern species supposed to have rounded Scotland. The invasion of *Brama raii* in the southern North Sea was less important in 1952 than in 1951, when 39 specimens were recorded, 35 of which between December 3 and 26 (2 specimens in January, 1952). The 1952-invasion took place earlier than that of 1951, presumably as a result of early cold.

It is gradually becoming clear that not only southern species are constantly on the move, but that the same holds to some extent for northern species. Their southern limit may shift from year to year. After the war it looked as if southern species in the southern North Sea had moved farther northward than previously and driven a number of northern species back. Since then, some northern species seem to have retaken their former place. In order to get more insight into such changes also northern species have been studied by Mr KRISTENSEN to some extent; they are mentioned in the list under numbers 16-23. *Onos cimbrius* is not rare on the Oystergrounds, but seldom found nearer our coast, presumably because of the higher summer temperatures there. *Scorpaena dactyloptera* is very rare in the southern North Sea, from where 7 specimens are now known to us. Two species, not mentioned in the list, are *Cyclopterus lumpus* and *Lophius piscatorius*. Adults of *Cyclopterus* were rather common in early spring 1952, juveniles were numerous in the Waddensea in the autumn. *Lophius* was more common than in the foregoing years: 14 specimens were received from the vicinity of Texel Hole; most of these were young (25-49 cm), only one was older (81 cm).

As in foregoing years, attention was also given to the Cephalopods. All of the species found in the southern North Sea are migrants, but they occur in different periods of the year.

A specimen of *Todarodes sagittatus* was recorded from Texel Hole on May 8, and 2 *Todaropsis eblanae* were brought in from the same area on January 24 and May 22. *T. sagittatus* is nearly always found washed ashore; its capture by fishermen (as in this case) is a rare event. *T. eblanae* is extremely rare in the southern North Sea. In addition to these, 2 specimens of *Octopus vulgaris* were received, one in November, the other in December, and 4 *Eledone cirrhosa*, 2 in May and 2 in December.

For reasons of continuity and for sustaining the supply of material to University courses 88 *Sepia officinalis*, several hundred *Loligo vulgaris* and a thousand *Loligo forbesi* were bought. Among the *Sepia*'s, the 1951 year-class was scantily represented. The 1951 year-class of *Loligo vulgaris* yielded 9 specimens in January (1952), this being a great exception; the species is a summer visitor to our coast (April-September); 18 young ones, hatched in 1952, were received between Sep-

tember and November. The number of older *Loligo vulgaris*-individuals was relatively small, young ones were probably more frequent than usual.

In connection with previous records, 10 *Portunus puber* may be mentioned; 4 came from the vicinity of Texel Hole, 6 from localities closer inshore. Further, 2 *Maia squinado* were also received from the vicinity of Texel Hole: a male with a carapace length of 14.1 cm on February 27, another male whose carapace length was 15.9 cm on November 25. Up to now, 3 records of this species are known to us from the North Sea.

Finally, the increase in southern direction of *Nephrops norvegicus* should be mentioned. After the severe cold of early spring, 1947, the species had only one centre of occurrence in the vicinity of the Dutch coast, which was situated in Botney Gut, south of the Dogger. In the ensuing years it spread more and more in southeastern direction, until in 1952 2 specimens were caught in the Schulpengat near Den Helder. The following numbers were received from the vicinity of Texel Hole since 1947:

1947	none	1950	5
1948	none	1951	4
1949	1	1952	17

These records lead us to believe that, besides soft bottoms, severe winters are the main cause of the restricted occurrence of this species in the southern North Sea.

The hydrographic investigations under the direction of Mr POSTMA dealt mainly with two questions: the cycle of nutrients in the Wadden Sea, and the chemical composition of suspended matter.

In previous years the study of nutrients was chiefly restricted to inorganic and organic phosphorus. This study, together with observations on water movement and suspended matter, resulted in a better understanding of the basic principles of the cycle of organic matter in the Wadden Sea. In order to obtain more detailed information on this subject, the cycle of inorganic nitrogen compounds was included in the research in 1952. Besides, the study of the cycle of chlorophyll, already started in 1950, was continued in the course of 1952. It is hoped that in this way a more or less complete picture of the production of organic matter will be gradually developed.

The chemical analysis of the suspended matter of the Wadden Sea was started by Mr SCHEELE of the Rijkswaterstaat, when he was on duty at our Station during the period 1936-1945. After the war, attention was first given to water movements and the distribution of suspended matter over the Wadden area as a whole, without entering into the details of the composition of the suspended material. In the present state, however, a more extended knowledge of this composition

is again felt necessary, especially in connection with seasonal and geographical differences and with the results of our investigations on molluscs. The analyses are now carried out by Mr BEKE, analyst to the Station.

It will follow from a later part of this report that Mr POSTMA participated in a combined geological and hydrographical expedition to the Caribbean Sea. In connection with his work at Den Helder, a study was made of the transport of suspended matter carried into the Caribbean by the Orinoco river. Certain aspects of this investigation may shed light on Wadden Sea problems.

Relatively much time and attention was given to the study of salinity and oxygen content of the Nieuwediep, the harbour of Den Helder, from where the Station pumps its sea water. This inquiry was made as a result of the partial closure of the harbour in 1951. The question will be treated in fuller detail below.

The investigations of Dr TAMMES, concerned with the influence of waste water disposal on life in the sea, made good progress. The work included the study of several species. The uptake and removal of organic poison in the animal body was studied for different ages and at different temperatures. Also the disappearance of poison in the sea made part of the program. The primary importance of the results lies, of course, in the possibility of their application, but the purely scientific aspects give these results an interesting background. Dr TAMMES' great technical ability, moreover, proved of much value to other workers at the Station.

Before leaving this part of our report, concerned with research proper, mention should be made of a grant made by the Netherlands Organization for Pure Research for an inquiry into lunar influence on the reproductive cycle of marine animals. The application for the funds had been made by Dr KORRINGA and the undersigned and the research will be carried out at the Zoological Station by Mr DE BLOK.

The summer courses, given at the Zoological Station in 1952, were attended by 22 students. The total number of man-days for individual investigators and summer course participants was 736; the number of individual workers was rather large, the average duration of their stay was short. The total number of visitors was not small, but, still, there was a decline since previous years. This situation in our opinion reflects the growing possibility for biological specialisation in our country. In addition, there is perhaps a growing inclination for institutions working on applied problems to obtain their scientists at an early age.

Close cooperation was maintained with several authorities: the

Rijkswaterstaat, the Government Institution for Fisheries Research, the Royal Netherland Meteorological Institute, the Government Institution for Waste Water Research, University laboratories, etc. The German research vessel "Gauss" visited Den Helder in the beginning of March. The English fisheries research vessel "Sir Lancelot" and the Dutch research vessel "Anthony van Leeuwenhoek" payed a visit simultaneously. On board the "Gauss" as well as in the Zoological Station a survey of some aspects of marine research now carried out by England, Germany, and the Netherlands, was given. The Netherlands Zoological Society held a meeting at Den Helder on the 19th and 20th of September. On that occasion a general account was given of the results obtained at the Station since 1932. Six investigators gave lectures concerning their special fields of study. Apart from these occasions, the Zoological Station was visited by a small number of foreigners.

For several reasons upkeep and repair of the building were rather neglected. This was partly due to an attempt at general economy, so that more money could be spent on the cutter "Max Weber" for a new crank-shaft; partly, to the fact that the handiman during the summer months was burdened with additional duties. Repairs inside the building, which can be carried out in winter, are easier to accomplish than outside upkeep, which should preferably take place in summer. In the autumn of 1952 most of the flooring in the building was varnished, several carpentry repairs were made and so forth.

The new aquarium functioned well and will be a valuable addition when it becomes available for our own research. The aquarium was supplied with a glass roof in order to ensure an adequate light supply. We have in this way consciously accepted the possibility that the maintenance of a somewhat constant temperature would be difficult. Our reasoning was that in summer the temperature could be modified by whitewashing the windowpanes, whereas in winter it could be accomplished by heating. Contrary to our expectations, the summer temperature rose higher than is desirable, but the winter temperature never fell too low. For the present experiments we are using four 1.5 K.W. electromotors. Part of their energy is turned into heat, which is accumulated in the water, well isolated in the subterranean tanks. The cooling of the water hardly keeps pace with the development of heat and even in periods of frost the water temperature hardly sinks below about 8°C. Fortunately, the aquarium in its final form will be in much better condition than now, because only one motor will be used. Still, difficulties in maintaining low enough temperatures in summer may be anticipated.

The repairs of the "Max Weber", already mentioned in the pre-

vious annual report, lasted until May and cost much more than anticipated, because the insurance refund was lower than expected. Part of this additional cost was overcome by economising on other items in the budget, part of it was paid by the Government. From May onward, the "Max Weber" was rather regularly in use. Either the ex-engineer of the lifeboat, Mr EELMAN, or our own technician, Mr PRINS, acted as skipper. During the second half of 1952 the ship underwent a thorough overhaul, so that it was in satisfactory condition at the commencement of winter.

There were few changes in personnel. In the place of Mr PIJL, who left for New Zealand, Mr BEKE was appointed analyst from February 1st onward, whereas Miss H. NAGTEGAAL, who left for Australia, was replaced by her sister C. NAGTEGAAL. Mr POSTMA, as already mentioned, participated in a research expedition to the Caribbean Sea, organized by Royal Dutch Shell, from April 1 to July 1. Thereafter, he visited the United States, especially Scripps Institution of Oceanography at La Jolla, California, and Woods Hole Oceanographic Institution at Cape Cod, Massachusetts. His salary, which was then available for other purposes, was partly used for the temporary appointment of Mr DE BLOK.

The Station's personnel at the end of 1952 consisted of:

Dr J. VERWEY, Director

I. KRISTENSEN, Biological research and supply of materials

Dr J. WESTENBERG, Biological research and library work

H. POSTMA, Hydrographic research

Miss T. STOLL, Administrator

N. PRINS, Technician

M. BUHRE, Handiman

A. DRAL, Biological analyst

CH. BEKE, Chemical analyst

Miss C. NAGTEGAAL, Student analyst

T. DE BOER, Student analyst

Vacant, Resident caretaker-skipper and wife

Mrs D. FERNHOUT-GLAS, Char woman

Dr P. M. L. TAMMES, Applied biological research, paid by industry

G. VAN DER WAL, Student analyst for Dr TAMMES' research.

The library conditions have improved since Dr WESTENBERG took the responsibility of its care in 1951. Several pre-war exchange relationships were resumed. In addition, a number of new exchange agreements were reached. It was attempted to fill up gaps in the files. Much attention was also given to the binding of periodicals. Some new books were purchased, but the small library budget hardly permits expenses in this direction. A word of thanks is extended to

those inside and outside the Society, who furnished the library with books or reprints. The lack of space for the library, which has been mentioned in several annual reports, is becoming more and more severe, and it is hoped that the Society will succeed in finding a solution for this difficult situation.

The supply of study material was, according to our own notions, rather important. The receipts were about fl 4300.—, in which "Artis", the Amsterdam Zoo, took an important part. The purchase of animals, including those for our own research and for aquarium food, amounted to about fl 3400.—, so that there was a surplus of fl 900.—. Up to this time, the cost of formalin, alcohol, etc. was never subtracted from the surplus. These costs in 1952 amounted to some fl 200.—, so that the profit realized was about fl 700.—.

The Government grant in 1951 amounted to fl 60 400.—; in 1952 it was about fl 66 800.—, in 1953 it is fl 70 000.—, whereas the budget for 1954, if accepted by the Government, will call for another increase. These increases have been brought about in the first place by periodic salary increases, but for 1954 there is included in the request a sum of fl 1200.— for a new custodian with additional duties as skipper on the "Max Weber", a sum of fl 1200.— for electricity for the new aquarium, and an additional sum of fl 6000.— for some expensive instruments.

It was pointed out in the previous annual report that the year 1951 ended with a deficit of fl 2822.48. When the repair costs of the "Max Weber" appeared to be so much higher than expected it was apparent that this additional expenditure could not be met within the 1952 budget. The Government then supplied the necessary financial aid to meet these costs and part of those for the vessel. Because of the high costs of the latter we were extremely economy conscious on other parts of the budget as well, with the result that the year 1952 ended with a deficit of less than fl 150.—. Once again, we should thank the Government for the support it is giving to marine biological research.

Finally, as in the previous report, a few words should be added concerning the construction of the new naval port in the immediate vicinity of the Station, which caused us much additional work. In September, 1951, the southern entrance of the Nieuwe Diep was closed and the surface salinity of this old harbour became much lower due to the entrapped fresh water, sluiced in from the North Holland Canal. The Royal Dutch Navy, whose Ministry had guaranteed us a supply of good sea water, utilised a water supply boat, which furnished us with salt water from the Marsdiep. In the spring of 1952 it was decided to lengthen the existing cast iron piping by a plastic part to the bottom of the harbour. Salt water could then be furnished directly

from below, in front of the Station. Before the piping had been laid, it appeared that the oxygen content near the bottom had fallen considerably and the laying of the piping was postponed. After some further months of study it was decided to lay the piping, because the operating costs of the supply boat during summer would be higher than the costs of the piping. The piping was then laid in October, and since that time the Station pumps its water from a depth of 8 metres, 1.5 metres above the bottom. We intend to use from now on the piping in winter, whereas during summer, should the oxygen content again decrease, a water boat will supply water for the aquaria. The total cost of the plastic piping and water boat has amounted at this time to about fl 25 000.—, which were paid by the Navy Department.

The oxygen content of the water pumped from the bottom of the Nieuwe Diep was abnormally low even in October, but it is brought to the level necessary for the aquaria through changes in the water circulation. As stated already, we do not expect this temporary situation to suffice in the summer months. This winter, however, a connection between the old and the new harbour has been made not far from the Zoological Station, and it is hoped that the oxygen content and salinity conditions may improve. The study of the condition of the water is therefore being continued.

Den Helder, February, 1953

J. VERWEY

THE DISTRIBUTION OF THE GENUS *DROSOPHILA* IN THE NETHERLANDS

by

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I. INTRODUCTION

During the past five years investigations concerning the distribution of the genus *Drosophila* in Europe show a remarkable progress. A vast amount of data has so far been collected for Switzerland (BURLA 1948, 1949, 1951), South and Western France, Spain and Portugal (BURLA and GLOOR 1952, HADORN *et al.* 1952) and Scotland (BASDEN 1952, 1954).

From the Netherlands with its typical lowland biotopes of polders, marshland, dunes and fluvioglacial sands with heathland and pine-forests hardly anything was known. For this reason a study into the distribution of the various species of the genus *Drosophila* has been started in our country in 1950. The first results were published in 1951 (LEVER and SOBELS); the data extending over the years 1950–1952 will be summarized here, special consideration having been given to the composition of the populations under different oecological conditions.

The flies were trapped by the method of PATTERSON (1943), using

¹ In collaboration with R. J. T. DUIVEN, M. HJINK, E. L. M. J. HOESSELS, J. P. KRUIJT and N. SPRONK.

tins placed on the ground which contained fermenting fruit of different kinds. After having been used for a few days the old bait was discarded and replaced by new. For identification the key of BURLA (1951), but also, though to a lesser extent, those of DUDA (1935) and PATTERSON (1943) were used.

The total number of flies which has been caught and identified throughout this investigation amounts to about 30.000.

Considering the various biotopes it is self-evident that the natural biotopes form the most interesting category. In a densely populated country like the Netherlands, however, pure, untouched wild spots are relatively rare. Therefore special consideration was also given to the populations of orchards which form such a characteristic feature of many a Dutch landscape. A number of gardens have also been sampled in those regions which have been studied more intensively.

II. NATURAL BIOTOPES

The various localities where flies have been collected are shown in fig. 1. They are discussed below and the most characteristic species are mentioned. A detailed record of the different trapping stations is given in table 1. A systematic grouping of more or less similar biotopes at different localities has been attempted. The arbitrary character of such a subdivision will easily be recognized, as on the other hand, a grouping of different types of trapping sites in the same locality was also thought to be desirable. The localities are indicated by numbers and the respective trapping sites at the same locality by letters.

A. DUNES AND COASTAL AREA

1. Huisduinen (28 VII–1 VIII, 1950). Pine plantation in dunes, with undergrowth of *Rubus*, *Sphagnum* and *Polygala*. *D. subobscura* dominating. Total of 354 specimens of 3 species.

2a. Loosduinen (5–18 VIII, 1950). Inner border of dunes planted with *Quercus*; undergrowth of *Betula*, *Sambucus*, *Rubus* and *Calluna*. *D. subobscura* dominating, high frequency of *D. phalerata*, *D. immigrans* common. Total of 136 specimens of 9 species.

2b. Inner border of dunes planted with *Pinus austriaca*, and *Quercus*; undergrowth of *Calluna*. *D. subobscura* dominating, *D. phalerata* frequent. Total of 69 specimens of 7 species.

3a. Near "Overduin", Oostkapelle, Isle of Walcheren (19–31 VII, 1950). Dunes 200 m from the sea with a vegetation of low bushes and shrubs consisting of *Sambucus nigra*, *Salix repens* and *Betula*; undergrowth of *Calamagrostis arenaria*, *Calluna*, *Jasione montana*, *Galium verum* and

TABLE I

The numbers of *Drosophila* trapped in natural biotopes.

N = number of individuals; % = relative frequency of the species; + = less than 0.5 %.

Euphrasia stricta. *D. subobscura* dominating; *D. melanogaster* very frequent; only record of *D. fenestrarum*. Total of 241 specimens of 8 species.

3b. Border of a wood on edge of dunes, ± 1000 m from the sea. For vegetation see 3 c. *D. subobscura* dominating, *D. phalerata* and *D. funebris* the next most frequent. Total of 732 specimens of 11 species.

3c. Coppice woodland behind the dunes, ± 1300 m. from the sea.



Fig. 1. The trapping stations in natural biotopes - 1. Huisduinen; 2. Loosduinen; 3. "Overduin" Oostkapelle; 4. "Berkenbosch" Oostkapelle; 5. Leuvenum; 6. Het Woold; 7. Soesterberg; 8. "Prattenburg" Veenendaal; 9. Bemelen (near Maastricht); 10. Lemiers (near Vaals); 11. Gagelpolder (Westbroek); 12. "De Hel" Veenendaal; 13. Oldeneel (near Zwolle); 14. Winterswijk; 15. Oedingse beek; 16. Jekerdal; 17. Geuldal.

Planted with *Fraxinus*, *Acer*, *Alnus*, *Sorbus aucuparia* and *Prunus padus*; undergrowth of *Rubus* and various ferns. *D. phalerata* dominating; *D. subobscura* less frequent. Total of 322 specimens of 11 species.

4a. Near "Berkenbosch", Oostkapelle, Isle of Walcheren 3-13 VIII, 1952). Coppice woodland with clearings, just behind the dunes,

± 350 m from the sea. Planted with *Acer*, *Betula*, *Prunus padus*. Undergrowth of *Teucrium scorodonium*, *Rubus*, *Epilobium* and various ferns. *D. subobscura* dominating; *D. tristis* very frequent; *D. obscura* common. Total of 167 specimens of 9 species.

4b. Forest walk behind the dunes, ± 400 m. from the sea. Planted with *Quercus*; undergrowth of *Alnus*, *Betula*, *Fraxinus*, *Sorbus*, *Rubus* and *Pteris aquilina*. *D. tristis* dominating; *D. subobscura* the next most frequent; *D. deflexa* common; 2 specimens of *D. cameraria*. Total of 1144 specimens of 14 species.

4c. Parkland, ± 450 m from the sea. Trees: *Quercus*, *Acer* and *Aesculus*; undergrowth of various shrubs. *D. tristis* dominating; *D. subobscura* the next most frequent. Total of 346 specimens of 9 species.

B. WOODLAND

5. Border of a wood, Leuvenum (3 VIII, 1952). Trees: *Quercus* and *Fagus*; undergrowth consisting of *Salix*, *Alnus*, *Betula*, *Myrica gale*, and *Urtica*. *D. subobscura* dominating; *D. phalerata* and *D. obscura* frequent. Total of 134 specimens of 9 species.

6. Forest, Het Woold near Winterswijk (3-31 VII, 1951). Trees: *Quercus*, *Alnus*, *Acer*, *Fagus* and *Fraxinus*; undergrowth consisting of *Lonicera*, *Prunus*, *Acer*, *Corylus*, *Rubus*. *D. subobscura* dominating *D. helvetica*, *D. phalerata*, *D. obscura* and *D. immigrans* common; *D. silvestris*. Total of 521 specimens of 14 species.

7. Fir-tree-heathland biotope, Soesterberg (1 VII, 1950). The border of a firwood on the edge of heathland with scattered birch trees. Almost exclusively *D. subobscura*. Total of 459 specimens of 4 species.

8. Border of a wood, near "Prattenburg", Veenendaal (3 VII, 1952). The border of a mixed wood on the edge of heathland and arable land. Trees: *Pinus*, *Fagus*, *Quercus*, *Betula*, *Alnus*; undergrowth consisting of *Rubus*, *Urtica* and various grasses. *D. subobscura* dominating; *D. melanogaster* and *D. hydei* frequent. Total of 477 specimens of 6 species.

C. OPEN AREAS

9. Bemelen, near Maastricht 18-21 VII, 1951). Open slope of a hill with scattered groups of trees and bushes consisting of *Rosa*, *Sambucus*, *Rubus*, *Crataegus* and *Salix*. Undergrowth characterized by an abundance of flowering plants as *Teucrium montanum*, *Ononis repens*, *Centaurea jacea*, *Hypericum perforatum*, *Agrimonia*, *Achillea*, *Rumex*, *Campanula*, *Clematis vitalba* and various Labiatae and Umbelliferae. *D. hydei* dominating; *D. subobscura* and *D. melanogaster* equally frequent. Total of 158 specimens of 3 species.

10. Lemiers, near Vaals (12 VII, 1951). Open grassland with scattered groups of trees and bushes, consisting of *Crataegus*, *Sorbus*, *Corylus*, *Betula*, *Fagus*; undergrowth of various grasses and *Ranunculus*, *Urtica*, *Rumex*, *Taraxacum* and *Bellis*. *D. subobscura* and *D. melanogaster* about equally frequent; high frequency of *D. hydei*. Though these small numbers do not permit any definite statement a certain similarity of the populations in localities 9 and 10 may be observed. Total of 144 specimens of 6 species.

D. MARSHLAND

11. Gagelpolder, Westbroek (5 VII and 6 IX, 1950). Small peat island dispersed in waterland with a vegetation of *Alnus*, *Rhamnus*, *Betula*, *Lonicera*, *Rubus*, *Phragmites communis* and *Sphagnum*. *D. melanogaster* dominating; *D. subobscura* next frequent; 1 specimen of *D. macularis*. Total of 145 specimens of 5 species.

12. De Hel, Veenendaal (26 VII, 23 IX, 1952). Peat and marshland with a vegetation of *Phragmites communis*, *Carex*, *Comarum*, *Salix* and *Alnus*. 26 VII, 1952: 32 specimens of which 16 *D. macularis*; 23 IX 1952: 95 specimens of which 3 *D. macularis*, *D. subobscura* dominating. In total 7 species.

13. Wooded marshland, Oldeneel (24-30 VII, 1951). Grassland bordered by a small wood consisting of *Populus* and *Salix*, with an undergrowth of *Salix*, *Alnus*, *Rosa*, *Urtica* and *Phragmites communis*. *D. subobscura* dominating; *D. phalerata* and *D. immigrans* common; 1 specimen of *D. macularis*. Total of 568 specimens of 15 species.

14. Het Woold near Winterswijk (20-25 VII, 1951). Marshland with isolated birch trees and willow bushes. Undergrowth of *Molinia*, *Erica*, *Drosera*, *Eriophorum* and *Sphagnum*. Almost exclusively *D. subobscura*. Total of 363 specimens of 4 species.

E. WATERCOURSES

15. Oedingsche beek (25-28 VII, 1951). The banks of a small stream with trees and bushes of *Quercus*, *Fraxinus*, *Carpinus* and *Corylus*; undergrowth of *Iris*, *Eupatorium*, *Verbascum*, *Carex*, *Urtica*, *Rubus* and *Galium*. Bad weather limited the catches. Mainly *D. littoralis*. Total of 40 specimens of 4 species.

16. The banks of river Jeker, Canne (VII and VIII, 1951, 1952). Vegetation consisting of scattered groups of trees and shrubs. Trees: *Populus*, *Fagus*, *Quercus*, *Corylus*, *Crataegus*, *Sorbus*, *Sambucus*, *Alnus*, *Rubus* and *Viburnum*. Undergrowth characterized by an abundance of flowering plants as *Vicia*, *Ranunculus*, *Papaver*, *Matricaria*, *Rumex*, *Convol-*

zulus, *Achillea*, *Hypericum*, *Trifolium*, *Symphytum*, *Ajuga* and *Valeriana*. *D. melanogaster* dominating; *D. subobscura* next frequent; *D. kuntzei* common; *D. rufifrons* (*nitens*). Total of 1336 specimens of 15 species.

17. The banks of the Geul stream, Meerssen (11-27 VII, 16-18 VIII 1951). Scattered groups of trees and bushes consisting of *Salix*, *Crataegus*, *Corylus*, *Alnus* and *Sorbus*; undergrowth: *Epilobium*, *Urtica urens*, *Myosotis palustris*, *Papaver rhoeas*, *Trifolium*, *Ranunculus*, *Alchemilla*, *Plantago media*, *Sonchus*, *Valeriana officinalis*, *Scrophularia*, *Matricaria*, *Ajuga reptans* and *Convolvulus arvensis*. *D. melanogaster* dominating; *D. subobscura* next frequent; *D. hydei* common; *D. polychaeta*. Total of 1082 specimens of 13 species.

III. ORCHARDS

Orchards cannot be considered as natural biotopes, but nevertheless they are of importance because of their uniformity of vegetation and microclimatological conditions.

The location of the orchards under consideration is shown in fig. 2. A (Oldeneel), B₁ and B₂ (Nunspeet), C (Houthem) and D (Caberg-Nielsen) were planted with apple and pear trees. E. (Caberg-Broecx) was a plum orchard. The results are shown in table II.

TABLE II

The numbers of *Drosophila* trapped in orchards. N — number of individuals; % — relative frequency of the species; + = less than 0.5 %.

Species	Oldeneel		Nunspeet				Houthem		Caberg Broecx		Caberg Nielsen		Total per species	
	A		B ₁		B ₂		C		D		E		N	%
	N	%	N	%	N	%	N	%	N	%	N	%		
<i>deflexa</i>	1	+	2	+	5	+	—	—	—	—	—	—	8	+
<i>busckii</i>	—	—	—	—	—	—	—	—	—	—	1	+	1	+
<i>melanogaster</i>	63	8	205	9	806	37	724	33	126	50	154	87	3465	37
<i>simulans</i>	—	—	1	+	4	+	—	—	—	—	—	—	5	+
<i>obscura</i>	5	1	266	12	185	8	2	+	—	—	—	—	458	5
<i>silvestris</i>	—	—	11	+	4	+	—	—	—	—	—	—	15	+
<i>tristis</i>	9	1	114	5	96	4	4	+	—	—	—	—	223	2
<i>bifasciata</i>	3	+	30	1	16	1	—	—	—	—	—	—	49	1
<i>ambigua</i>	2	+	—	—	—	—	—	—	—	—	—	—	2	+
<i>subobscura</i>	635	78	1079	50	814	37	1426	65	122	48	126	7	4202	45
<i>helvetica</i>	9	1	194	9	113	5	1	+	—	—	—	—	317	3
<i>transversa</i>	27	3	6	+	7	+	1	+	2	1	2	+	45	+
<i>phalerata</i>	31	4	97	4	76	3	8	+	—	—	—	—	212	2
<i>kuntzei</i>	1	+	117	5	9	+	2	+	—	—	11	1	140	1
<i>limbata</i>	3	+	—	—	—	—	1	+	—	—	—	—	4	+
<i>littoralis</i>	5	1	3	+	—	—	—	—	—	—	—	—	8	+
<i>funebis</i>	19	2	26	1	40	2	6	+	3	1	12	1	106	1
<i>hydei</i>	—	—	1	+	1	+	10	+	—	—	69	4	81	1
<i>immigrans</i>	4	+	18	1	22	1	19	1	—	—	—	—	63	1
Total per trapping site	817		2170		2198		2204		253		1762		9404	

It will be seen that *D. subobscura* and *D. melanogaster* are the two most common species in this biotope. A similar finding was recorded by BURLA (1951) for Swiss orchards, though there *D. melanogaster* predominates over *D. subobscura*. Moreover, the frequency of *D. funebris* is definitely lower in the Dutch orchards than in those studied by BURLA.



Fig. 2. The trapping stations in orchards – A. Oldeneel; B 1,2. Nunspeet; C. Houthem; D. Caberg-Broex; E. Caberg-Niessen.

Comparing the composition of the populations in the Northern localities with those of the South it will be noticed that the number of species occurring in the first is much higher. At A, B₁ and B₂, 15, 16 and 15 species respectively were collected; in the Southern localities C, D and E, 12, 4 and 7 species respectively. The populations of Nunspeet (B₁ and B₂) and those of Houthem (C) bear a certain similarity in their composition. Species like *D. obscura*, *bifasciata*, *tristis*, *helvetica*, *kuntzei* and *phalerata* are more common, however, in the Northern locality. It does

seem possible that such variations are due, at least in part, to different weather conditions during the collecting season in the two localities.



Fig. 3. The trapping stations in gardens – i. Den Helder; ii. Zeist; iii. Utrecht; iv. Lunteren; v. Oldeneel; vi. Nunspeet; vii. Veenendaal; viii. Caberg; ix. Geleen; x. De Bilt; xi. Oostkapelle; xii. Loosduinen.

IV. GARDENS

To complete our data on the distribution of the various species gardens were sampled at nearly all the localities where natural biotopes have been studied. The trapping stations are shown in fig. 3.

The following species listed in order of frequency have been recorded: *D. melanogaster*, *subobscura*, *obscura*, *helvetica*, *phalerata*, *funnebris*, *tristis*, *kuntzei*, *immigrans*, *bifasciata*, *transversa*, *simulans*, *littoralis*, *ambigua*, *rufifrons*, *hydei*, *limbata*, *busckii*, *testacea* and *histrion*. The majority of these

populations is characterized by a large number of species. Favourable oecological conditions thus are apparently provided for a large number of species by the varied vegetation as usually found in gardens.

V. THE INDIVIDUAL SPECIES

The revision of names of some species recorded here is based on studies of BASDEN, 1952 (*D. cameraria* Haliday = syn. with *pallidà* Zetterstedt) CAIN, COLLIN and DEMEREC, 1952 (*D. obscuroides* Pomini = syn. with *obscura* Fallèn) and HERTING, 1953 (*D. ruffifrons* Loew = syn. with *nitens* Buzzati; *D. deflexa* Duda = syn. with *Guyénoti* Burla).

Drosophila ruffifrons Loew 1873 (Syn.: *nitens* Buzzati 1943). Localities: 16, 17, III, IX.

This species has been recorded from some places in the middle and Southern regions of our country. The geographical distribution of the species seems of interest as it has been generally assumed that *D. ruffifrons* was a mediterranean species. From Switzerland BURLA (1951) records only two specimens, trapped in the Canton Waadt, North of the Lac Léman. HADORN *et al.* (1952) trapped the species in France, Spain and Portugal, predominantly in dry biotopes planted with cork oaks. No exact data are available about the biotope which is preferred by this species. In addition it may be mentioned here that the only natural biotopes where we observed the species were small rivers.

Drosophila deflexa Duda 1924 (Syn.: *Guyénoti* Burla 1948). Localities: 2b, 4b, 4c, 5, 13, 16, 17, A, B₁, B₂, V.

Small numbers of this species could be recorded from various biotopes.

Drosophila busckii Coquillett 1901. Localities: 2b, 3b, III, XII.

Corresponding to the observations of other authors this species was only recovered in the neighbourhood of human habitations. Its preference for mushrooms (see BASDEN, 1954) may be a reason that we did not trap the species on fermenting fruit baits.

On two occasions it was caught abundantly in houses, one of these being a chickenhouse, which seems of interest in relation to BASDEN's catches in a chickenhouse.

Drosophila melanogaster Meigen 1830. Localities: 2a-14, 16, 17, A-E, I-XII.

Records from nearly all trapping sites. Highest frequencies of this cosmopolitan and domesticated species were observed near houses. At

a relative short distance from houses (200 m), however, its frequency in the populations diminished to less than ten percent. Only in a few natural biotopes (11, 16, 17) *D. melanogaster* has been observed to dominate over *D. subobscura*; less wooded country with a high humidity seems to be preferred.

Drosophila simulans Sturtevant 1919. Localities: B₁, B₂, III.

PATTERSON (1943) suggested that in mixed populations with *D. melanogaster* the relative frequency of this species increases along a North-South gradient. This was verified in Switzerland by BURLA, who recorded only 15 specimens North and 587 South of the Alps. The findings of HADORN *et al.* do not corroborate this assumption, as in all Southern trapping sites of S.W. Europe the species only rarely has been observed. The authors, however, predominantly collected in natural biotopes and they explain the absence of *D. simulans* in their catches on its preference for human habitations.

In relation to these findings the exceptionally Northern distribution in Western Europe, as shown by our data is of interest. The species was caught in a garden in Utrecht (III) and in two orchards at Nunspeet (B₁ and B₂).

Drosophila obscura Fallén 1823 (Syn.: *obscuroides* Pomini 1940). Localities: 3a-8, 13, 16, A-C, I-VII, X-XII.

The species is common in natural biotopes, especially in deciduous woodland. In contrary to BURLA's and BASDEN's records for Swiss and Scottish woods respectively, where *D. obscura* was often observed as the dominating species, its frequency in the Dutch habitats never exceeds that of *D. subobscura*. A similar finding was recorded by HADORN *et al.* for *D. obscura* in S.W. Europe.

Drosophila silvestris Basden 1954 (Syn.: *Obscura* - X of BURLA (1951)). Localities: 6, B₁, B₂.

This species only recently described by BASDEN (1954) is, according to this author, the third most abundant of the Scottish species. BASDEN found it most frequently in deciduous woodlands and in an old oak park. BURLA who distinguished the species as *obscura*-X sampled it from similar habitats, though only 56 specimens out of a number of 21765 flies in total. The only natural biotope where we found *D. silvestris*, with a frequency of 10 out of 521 individuals, was an old forest of oaks mixed with other deciduous trees (6). It was also observed in apple and pear orchards at Nunspeet (B₁, B₂) with a frequency of 15 out of 4368 individuals. Its rare occurrence in the Netherlands and Switzerland thus strongly contrasts BASDEN's findings for Scotland. It therefore

seems possible that more Northern climatological conditions are favourable for maintenance and extension of this species. Records of BASDEN (personal communication) of Northern Norway speak in favour of this assumption.

Drosophila tristis Meigen 1830. Localities: 1, 2a, 3b-6, 10, 13, 16, 17, A-C, III-V, VII, IX, X, XII.

The species is widely distributed, but only trapped in small numbers. In deciduous woodland behind the dunes near Oostkapelle on the Isle of Walcheren in Zeeland (4b, 4c) it has been observed as the dominating species in the population, namely 776 specimens in a total of 1490 trapped individuals. A similar observation has hitherto never been made (cf. also HADORN *et al.* p. 156).

Drosophila bifasciata Pomini 1940. Localities: 2a, 2b, 3b, 4a-6, 16, A-B₂, I, III, VI, XI, XII.

This species is widely distributed especially in the natural biotopes, but only occurs in small numbers. In some instances, however, it may have been confused with *D. obscura*. Our observations agree with those of BURLA (1951) and HADORN *et al.* (1952) for Switzerland and S.W. Europe, respectively.

Drosophila ambigua Pomini 1940. Localities: 3a-4c, 6, 13, A-B₂, III, VI, XII.

The distribution of this species in natural biotopes is much like that of *D. bifasciata*. According to HADORN *et al.* it shows a preference for dry mediterranean biotopes. Small numbers have also been recorded from Scotland by BASDEN (1954).

Drosophila subobscura Collin 1936. Recorded from all trapping sites.

D. subobscura is without doubt the most commonly distributed species in the Netherlands. The same statement has been made for Switzerland by BURLA (1951), for South-Western Europe by HADORN *et al.* (1952) and for Scotland by BASDEN (1954). With the exception of 3c, 4b, 4c, 11, 16, 17, D and E this species dominated at all sites. The first three numbers refer to samples from dunewoods in Oostkapelle where *D. phalerata*, respectively *D. tristis* dominated (see p. 359-360). The other localities are in South-Limburg (Southern Netherlands). The relative low frequency of the species in the latter area might be due to the fact that here trapping mainly was carried out during the day-time, whereas *D. subobscura* occurred in abundance particularly at sunset.

Drosophila helvetica Burla 1948. Localities: 5, 6, 13, 14, 16, A-C, III-VI, VII, X.

According to BURLA (1951) and HADORN *et al.* (1952) this species preferably lives in immature woodland with a high humidity. The same was observed in our country. The species occurs with a lower frequency than in Switzerland, though in an old forest of oaks and other deciduous trees in the East of the Netherlands (6) 57 specimens were observed in a total of 521 collected individuals.

Drosophila transversa Fallén 1823. Localities: 1-3c, 4b, 6, 7, 13, 14, 16, 17, A-E, III, V, IX, XI.

This species is widely distributed but has only been sampled in small numbers. It was mainly found in woodland which is in accordance with the observations of DUDA (1935), BURLA (1951) and BASDEN (1954).

Drosophila phalerata Meigen 1830. Localities: 2a-4b, 5, 6, 8, 10, 12, 13, 15, 16, 17, A-C, III-VII, IX, XI.

In the Netherlands this species is undoubtedly the most common one of the Quinaria-group. It occurs predominantly in woodland biotopes composed of various deciduous trees. Inside coppiced woodland behind the dunes on the Isle of Walcheren (3c) 242 specimens out of a total of 322 *Drosophila* individuals were collected. Our observations are in accord with those of BURLA (1951), HADORN *et al.* (1952) and BASDEN (1954).

Drosophila kuntzei Duda 1924. Localities: 2a, 3c, 4b, 6, 10, 12, 13, 15, 16, 17, A-C, E, III-VI, VIII, XII.

This species is rather limited in its occurrence. According to BURLA (1951) *D. kuntzei* is characteristic for young woodland. On the banks of the river Jeker (16) near Canne and in an orchard at Nunspeet (B₁) it has been collected in a relatively high proportion to other species. Near both localities there were, however, deciduous trees in the direct neighbourhood. *D. kuntzei* has not been recorded from Scotland (BASDEN).

Drosophila limbata von Rosen 1840. Localities: 13, 17, A, C, III, V, IX.

This is a very rare species. Similar statements have been made by DUDA (1935), BURLA (1951) and HADORN *et al.* The species is not known from Scotland.

Drosophila littoralis Meigen 1830. Localities: 4a, 4b, 13, 15, 16, 17, A, B₁, III-V, VII-X.

The species is rather rare in the Netherlands. It was predominantly observed in the neighbourhood of water. This is in accordance with the findings of BURLA (1951), HADORN *et al.* (1952). Its preference for biotopes with running water is confirmed from the records at site 15 at

the stream of Oedingen in the Eastern-Netherlands where 21 specimens were collected out of a total of 40 individuals (see also locality 16, along the Jeker stream).

Drosophila testacea von Rosen 1840. Localities: 6, 16, III, IV, XII.

This species is very rare in the Netherlands.

Drosophila funebris Fabricius 1787. Localities: 2a, 3a-3c, 4b, 4c, 6, 11, 13, 16, 17, A-E, I-XII.

The species has been sampled from nearly all the localities so far investigated. It shows a pronounced preference for human settlements. In natural biotopes the numbers are in general low, with the exception of sites 3b and 4c on the Isle of Walcheren; locality 4c however, was only at a short distance of a country house.

Drosophila hydei Sturtevant 1921. Localities: 3c, 8-12, 16, 17, B₁-C, E, III, IV, VI, VII-X.

This species seems characteristic of the localities in the South (9, 10, 16, 17), where it was trapped in high numbers. In other parts of the country it was only rarely observed with the exception of the border of a wood on the edge of heathland and arable land near Veenendaal (8). A certain preference for open areas seems to be suggested by our data. In the natural biotopes, investigated by HADORN *et al.* it was almost completely missing. Its cosmopolitan distribution is discussed by BURLA (1951).

Drosophila immigrans Sturtevant 1921. Localities: 2a, 3b-6, 8, 12, 13, A-C, II, III, V-VII, IX-XII.

This cosmopolitan species seems to be very rare in Switzerland. BURLA (1951) therefore states: "Schweiz, Nördlich der Alpen sehr selten und wahrscheinlich nur sporadisch auftauchend". From S.W. Europe only a very few specimens were recorded by HADORN *et al.* As these authors exclusively trapped in natural biotopes they ascribe its absence to the fact that *D. immigrans* is a domestic species. BASDEN (1954) found this species in Scotland only in banana stores.

Contrary to these observations the data of table 1 show that in the Netherlands *D. immigrans* is not at all uncommon.

In natural biotopes, its average frequency is about 2-3 percent. Highest frequencies were actually recorded in woodland or in the neighbourhood of woodland (2a, 4b, 6, 13). In gardens the species is very common, so that it sometimes dominates in these populations (samples from the same garden in Utrecht (III) in different months of the summer showed a considerable increase of *D. immigrans* in September).

According to SPENCER (1940) the species occurs in North-American populations predominantly in those biotopes where *D. hydei* is dominant. This phenomenon was not observed in our country (see table 2).

Drosophila histrio Meigen 1830. Locality: III.

Only two specimens were trapped in gardens in the town of Utrecht. This seems of interest as in Switzerland BURLA (1951) only sampled the species from natural biotopes.

Drosophila fenestrarum Fallén 1823. Locality: 3a.

Only one specimen trapped in a dune biotope at a distance of 200 m from the sea. According to DUDA (1935) *D. fenestrarum* is very common in Sweden. BURLA records only one specimen from Switzerland. HADORN *et al.* only found the species in Portugal. BASDEN (1954) and others collected it in Scotland, mainly by sweeping with a net. As he states, however, *D. fenestrarum* is not attracted to the usual types of *Drosophila* baits.

Drosophila macularis Villeneuve 1921. Localities: 11, 12 13.

So far only a few specimens of this species have been recorded, namely from Blain (Loire Inférieure), Rambouillet, Berlin, Budapest and Stadlau (DUDA 1935). We found *D. macularis* only in biotopes where reeds (*Phragmites communis*) grow. In "de Hel" near Veenendaal (12) 18 specimens out of a total of 127 collected individuals were obtained. Our observations thus are in full agreement with DUDA's statement that this species only occurs in marshland with an abundance of reeds.

After completion of the manuscript a sample from marshland near Amsterdam (Botshol) has been examined. There we found 6 *D. macularis* out of a total of 1432 specimens.

Drosophila cameraria Haliday 1833 (Syn.: *pallida* Zetterstedt 1847). Locality: 4b.

Only two specimens of this species were obtained in a wood behind the dunes near Oostkapelle (Walcheren). BURLA (1951) caught only one specimen in Switzerland. HADORN *et al.* (1952) did not find it rare in S. W. Europe; at some places they observed very high frequencies. BASDEN (1954) mentions it for Scotland. As the species only breeds in mushrooms its apparently rare occurrence in the Netherlands may be due to the fact that mushrooms were not investigated.

Drosophila polychaeta Patterson and Wheeler 1942. Locality: 17.

The first European specimen of this species is a female trapped near Meerssen at the Geul stream, South Limburg (27 VII, 1951). PATER-

SON and WHEELER (1943) sampled the species only from banana wharfs near Galveston, Texas, but assumed it to have immigrated from South, or Middle America. Another record is from the Hawaiian Isles and Guam (PATTERSON, personal communication). BASDEN (see SOBELS and BASDEN, 1953) found it on ships from West-Africa and Malaya at Liverpool. This shows how this apparently cosmopolitan species can become distributed.

Most strikingly the specimen recorded here was caught in scattered woodland remote from houses, ± 160 km from the sea. In addition it may be noted that the district of South Limburg is much frequented by excursionists from the big towns in the West. Banana peels left behind by such people might be responsible for its unexpected appearance at this wild spot.

VI. SPECIFIED DATA ON SOME SPECIES

Some preliminary observations of oecological work which is now under way, may be mentioned here.

1. Seasonal shifts in the composition of the populations.

TABLE III
Seasonal variation in two populations of gardens in Utrecht.

Species	Site A				Site B			
	July		September		July		September	
	N	%	N	%	N	%	N	%
<i>rufifrons</i>	—	—	—	—	1	—	1	—
<i>busckii</i>	—	—	1	—	—	—	1	—
<i>melanogaster</i>	54	8	245	42	66	18	109	31
<i>simulans</i>	—	—	—	—	4	—	2	—
<i>obscura</i>	4	—	4	—	12	3	6	2
<i>tristis</i>	—	—	1	—	1	—	6	2
<i>bifasciata</i>	—	—	—	—	—	—	1	—
<i>ambigua</i>	—	—	—	—	2	—	1	—
<i>subobscura</i>	569	86	179	31	246	68	192	54
<i>helvetica</i>	—	—	5	—	1	—	9	3
<i>transversa</i>	—	—	1	—	—	—	—	—
<i>phalerata</i>	—	—	7	1	26	7	16	4
<i>kuntzei</i>	1	—	1	—	—	—	—	—
<i>limbata</i>	1	—	1	—	—	—	—	—
<i>littoralis</i>	—	—	—	—	1	—	—	—
<i>junebris</i>	35	5	5	—	—	—	3	—
<i>hydei</i>	—	—	4	—	—	—	1	—
<i>immigrans</i>	—	—	125	22	—	—	8	2
<i>histrion</i>	—	—	1	—	—	—	—	—
Total	664		580		360		356	

In order to study the changes in the composition of populations during the main breeding season samples were taken at the beginning of July and in September at two trapping stations in Utrecht, the results of which are shown in table III.

The data suggest that in the course of the summer *D. melanogaster* numerically increases, whereas *D. subobscura* tends to decrease. *D. immigrans* also shows an increase which was confirmed at another site. Moreover, the total number of species present in these populations increases, namely at locality A from 6 to 14 and at locality B from 10 to 14 species. This phenomenon is probably a consequence of more favourable breeding conditions during the warm months of the summer.

2. Activity at different hours of the day.

HADORN *et al.* (1952) compared the activity of certain species in the morning and the evening. At seven different sites they sampled totals

TABLE IV
A comparison between morning and evening trapping at site 4b.

Species	Morning	Evening	$\frac{\text{Morning}}{\text{Evening}}$
<i>deflexa</i>	17	28	0.6
<i>subobscura</i>	71	169	0.4
<i>obscura</i>	48	47	1.0
<i>tristis</i>	155	457	0.3
<i>immigrans</i>	41	20	2.0

of 4719 individuals in the morning and of 4427 in the evening. The following statements are based on these observations. *D. tristis* shows a significant preference for the morning and *D. melanogaster* for the evening, whereas the other species observed are in their behaviour intermediate between these two extremes. *D. obscura*, *bifasciata*, *phalerata* and *kuntzei* were more frequently caught at the beginning and *D. subobscura* at the end of the day.

A similar observation has been done at locality 4b. There we trapped 359 individuals in the morning and 763 at the beginning of the evening. The numbers of the most abundant species and the ratio of the numbers trapped in the morning and in the evening are shown in table 4.

It will be seen that *D. deflexa*, *subobscura* and *tristis* show a greater activity in the evening, whereas *D. immigrans* was caught in greater numbers during the morning. *D. obscura* apparently has no distinct preference for either morning or evening.

At another site an hour by hour sampling of *D. subobscura* (1400 specimens) showed two peaks of activity for this species, namely one between 9 and 11 a.m. and one between 4 and 6 p.m.; greatest activity was, however, observed at the second peak.

As far as *D. subobscura* is concerned our results thus seem to be in line with those of HADORN *et al.* *D. tristis*, on the other hand, behaves quite differently in this population, than in those investigated by the Swiss authors. But it should be mentioned that in view of the relatively small numbers not too much significance can be attached to the results discussed above. Moreover, temperature, humidity and intensity of illumination presumably all influence the activity of these flies. As it certainly would be of interest to know how the activity of the flies varies in conjunction with these factors such investigations are now underway.

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VII. SUMMARY

1. To study the distribution of the genus *Drosophila* in the Netherlands samples were taken at various natural biotopes, orchards and gardens throughout the country. A total number of about 30.000 flies has been collected. The vegetation characteristic for the different trapping stations is briefly discussed.

2. In addition to the 12 species which in 1950 were collected for the first time in the Netherlands *Drosophila rufifrons* (Syn.: *nitens*), *D. silvestris*, *D. simulans* and *D. polychaeta* are here reported as new for the Dutch fauna.

3. Separate records on the distribution and biotope preferences are given of the following species.: *D. rufifrons*, *deflexa*, *busckii*, *melanogaster*, *simulans*, *subobscura*, *obscura*, *silvestris*, *tristis*, *bifasciata*, *ambigua*, *helvetica*, *transversa*, *phalerata*, *kuntzei*, *limbata*, *littoralis*, *testacea*, *juncbris*, *hydei*, *immigrans*, *histrio*, *fenestrarum*, *macularis*, *cameraria* and *polychaeta*. The occurrence of these species in the Netherlands is compared with their distribution in other parts of Europe.

4. Incidental observations on the biology of certain species suggest that in the course of the summer *D. melanogaster* and *D. immigrans* numerically increase, whereas *D. subobscura* decreases. *D. deflexa*, *subobscura* and *tristis* were found more active in the evening and *D. immigrans* in the morning.

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ASPECTS OF
DIAPAUSE IN ADULT INSECTS
WITH SPECIAL REGARD TO THE COLORADO BEETLE,
LEPTINOTARSA DECEMLINEATA SAY¹

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In temperate and cold zones the majority of terrestrial animals have to face the problem how to survive the cold season in a condition of slight activity. In the tropics, the same applies with regard to the dry period. In those species which, owing to special arrangements, are able to feed themselves during these periods, the activity of the gonads is arrested; reproduction synchronizes with the favourable season.

With regard to insects, distinction has for a long time been made between two groups, in which this synchronization would occur in two different ways. In *homodynamic* species, development and activity are directly inhibited by low temperature, drought, lack of food, to be again resumed on the return of physiologically favourable conditions. *Heterodynamic* species apparently pass on spontaneously to a condition of rest. In most cases this occurs before unfavourable environmental factors set in and is not simply terminated when these disappear². The two groups are not so strictly separated as their name-giver ROUBAUD (1922) supposed; transitions occur. Since HENNEGUY (1904) the condition of quiescence or arrested development has been named *diapause*. This phenomenon has several aspects: ecological, evolutionary, morphological, and physiological. We shall confine ourselves to the latter.

Diapause is not a clearly-defined physiological conception. It may occur during embryonic and postembryonic development and during

¹ Investigation supported by the Institute for Phytopathological Research (I.P.O.), Wageningen, The Netherlands.

² Since this communication was made, we have found that in *Leptinotarsa* the photoperiod, in combination with temperature, is the decisive factor for entering into diapause.

adult life, but in different species always at the same, precise moment. In embryos it may occur during different stages of development; in the larva just before emergence from the egg, or shortly before pupation. During inactive stages (egg, pupa) we observe arrest of growth and differentiation which may last for months and is not terminated until exposure to certain critical low temperatures takes place. In active stages (larva, adult) the arrest is preceded by an introductory behaviour (increase of nutrition, swarin formation, search for hibernation quarters). Changes in behaviour also persist during diapause itself.

In adult animals the activity of the gonads is arrested.

One is inclined to ask which elements diapause has in common in all these cases. These elements are:

1. Standstill of morphogenesis.
2. Strongly reduced basal metabolism. The fact that the rate of basal oxygen consumption is 50% or less as compared with that in the active condition applies to eggs (BODINE 1932), pupae (HELLER 1926, AGRELL 1951) and adults (NECHELES 1924, FINK 1925, MARZUSCH 1952).
3. Low water content, strong fat deposit.

In the pupae of some species of moths it appears that the reduced metabolism is caused by fundamental changes in the respiratory enzyme systems. It is not our intention to dwell on this interesting phenomenon at present.

In the following lines we are only concerned with diapause in adults, and especially with the Colorado Beetle, *Leptinotarsa decemlineata* Say.

In the Netherlands this beetle oviposits from May till August. The larva moults three times whereafter it goes into the soil to pupate. Two weeks later the adult of the first generation emerges, occurring over a period extending from July to September. During warm summers a varying though small number of these beetles starts oviposition. The greater part, however, re-enters the soil after a short period of intense food intake and strong fat deposition. Beetles may already be found underground in the beginning of August.

When taken indoors and kept at room temperature an increasing number of beetles emerges from the soil over a period extending from December to April. They are now able to take in food and, under suitable conditions, may begin to lay eggs.

In physiological terms these phenomena may be described as follows: In these beetles changes take place regarding animal as well as vegetative functions. An overall control mechanism must be present, which coordinates different functions in such a way as to first produce the resting stage and afterwards the state of reproduction. We shall describe some of these changes during pre-and postdiapause.

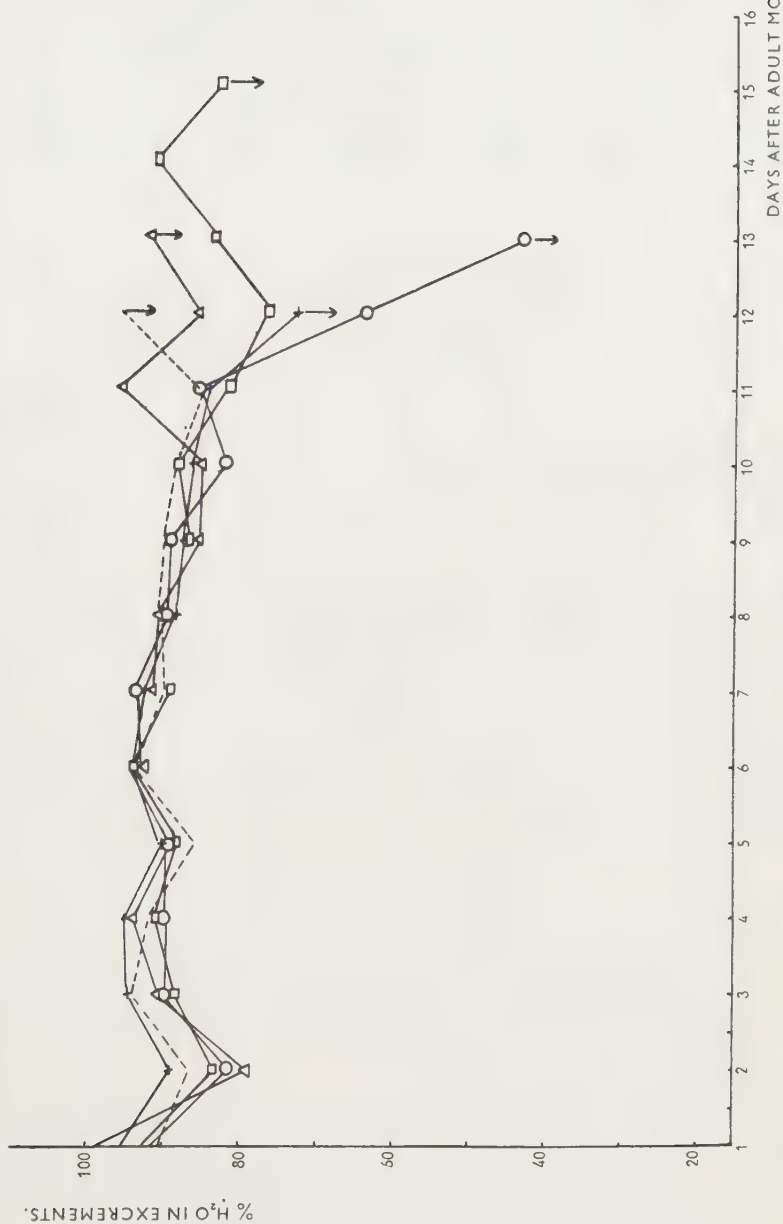


Fig. 1. Water content of the excrements produced by 5 beetles during pre-diapause. The arrow indicates the moment of entering into diapause.

I. WATER RELATIONS

In his famous monograph, TOWER (1906) mentions that the beetle, shortly before entering into diapause, excretes a large quantity of water with the excrements and, in so doing, loses an average of 27 % of its body weight. FINK (1925) describes a fall in water content (76 % at the beginning of pre-diapause, 59 % at the end, 56 % at the time of burrowing). A similar difference was found by BUSNEL (1939) and by ourselves (Table I).

TABLE I

Mean values of H₂O and fat contents as obtained in 4 determinations on 10 beetles each. Fat extraction by Soxhlet apparatus. The amount of free fatty acids was negligible.

	Tot. weight mg.	Fat content % of fresh weight.	H ₂ O content % of fresh weight.	Fat content % of dry weight.	Tot. H ₂ O mg.
after adult moult	759.6	2.0	78.7	9.8	598.1
6 d. prae-diapause	1044.1	4.0	71.0	10.1	738.4
4 months diapause	917.1	10.1	61.3	25.5	563.9

In our own experiments we daily determined the weight of 10 animals during pre-diapause. We also determined the quantity of leaf taken in and the weight and dry-weight of the excrements. The experiments were carried out in a constant temperature room at 25° C., R.H. 96 %, illumination 3000 Lux during 10 hrs. p. d.

At the end of pre-diapause the water content of the excrements was lowered rather than increased. (Fig. 1). There was nothing to indicate a sudden rise in water excretion. Nor does the course of body weight give an indication of this (Fig. 2).

II. BEHAVIOUR

The most conspicuous change of behaviour may be seen in the cessation of food intake and in the digging-in at the end of pre-diapause. When the animals do not have sand or other granular material at their disposal, but e.g. layers of filter paper, they install themselves underneath and become immobile.

Using primitive methods, BREITENBECHER (1918) investigated the reactions to light and gravity. Phototaxis was studied by placing the animals in glass tubes which were partly exposed to sunlight; the geotaxis was examined by placing them in gauze cylinders in a dark room. Creeping upwards indicated negative phototaxis. In this way BREITENBECHER found a positive phototaxis and a negative geotaxis

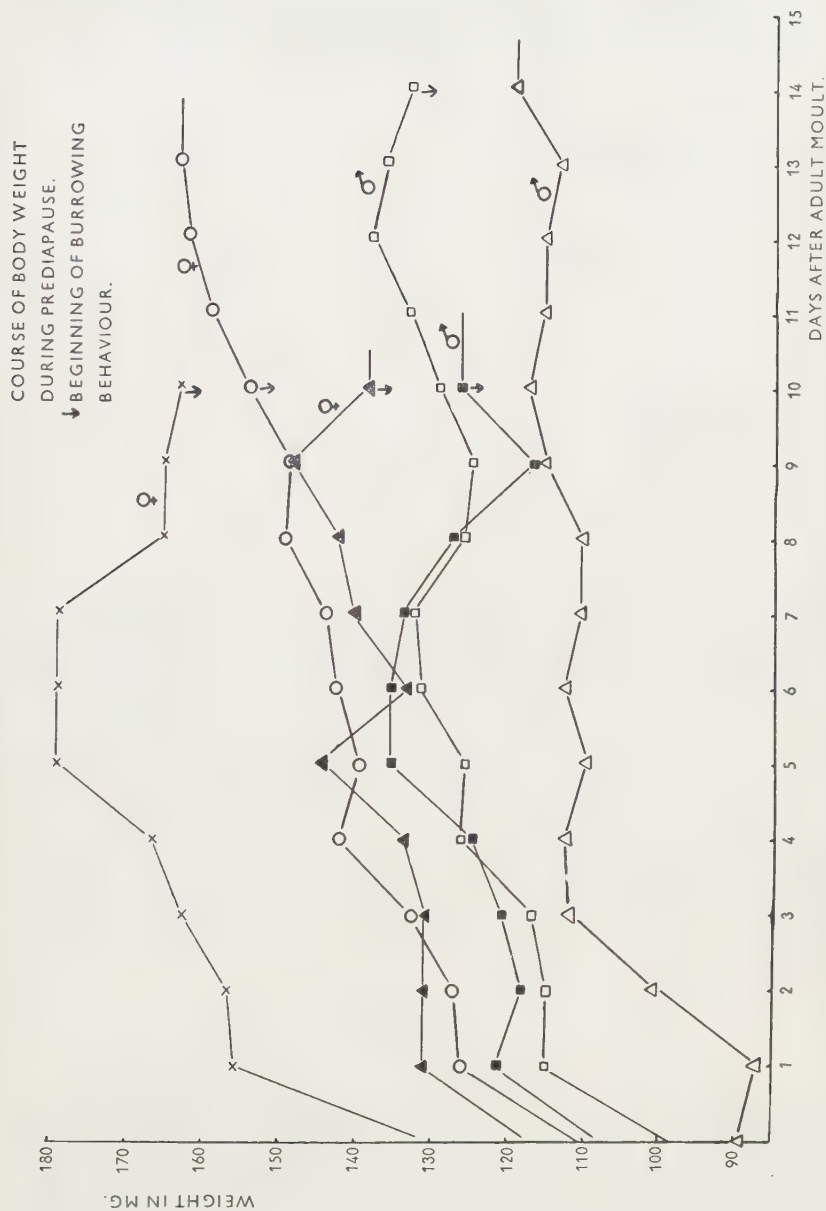


Fig. 2. Course of body weight during pre-diapause. ↓ = beginning of burrowing behaviour, when the animals are placed upon soil. Note that, when placed upon food, these animals can still feed and grow.

in active beetles, a negative or indifferent phototaxis and a positive geotaxis during diapause.

It seemed important to us to verify this by the use of more exact methods and to follow closely the changes during prediapause.

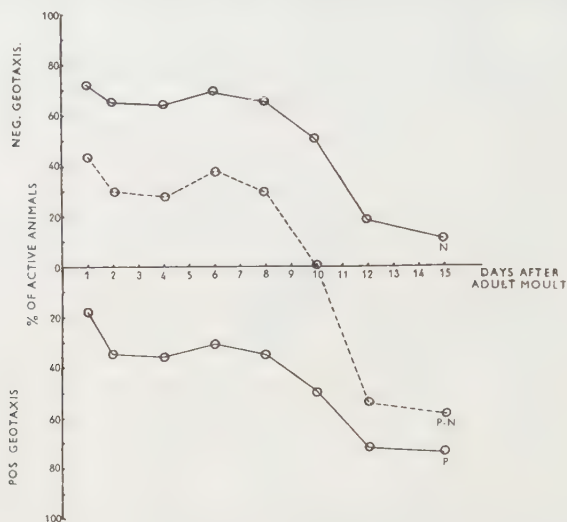


Fig. 3. Course of geotaxis during pre-diapause. The straight lines give the percentages of negative, resp. positive choices in each experiment. The broken line gives the mean value. Each point is obtained from 10 choices made by 10 animals each.

To this purpose an apparatus was constructed in which both photo- and geotaxis could be studied. For the study of geotaxis the choosing-chamber was placed at an angle of 30° . Twenty beetles were used in each experiment, carried out in duplicate by alternately turning left and right side upwards. The result is shown in the diagram (Fig. 3).

From this it is apparent that on the 6th–12th day of pre-diapause (at 25° C.) a transition occurs from negative to positive geotaxis. A similar shift in phototaxis is apparent. This is most obvious in the % of negative choices (Table II).

III. INFLUENCE OF TEMPERATURE ON BREAK OF DIAPAUSE

During several winters we carried out experiments in our serial thermal cabinet in order to study the influence of low-temperature treatment on the termination of adult diapause. Our conclusion was that a treatment of 42 d. at 5° C. postpones instead of accelerates the termination of diapause (DE WILDE, 1949). We now studied the effect of a rise in temperature. By a treatment with a temperature of $29\text{--}30^\circ$ C. and a

TABLE II

Change in phototactic behaviour on break of diapause obtained by exposure to 30° C. during 21 days. P-value determined by Student's method. Note that the decrease of negative choices is most obvious. Each number is the mean of 10 choices made by 10 animals. I = illuminated side; C = centre; D = dark side of apparatus.

% negative choices.

I.	illumination gradient (Lux) C.	D.	in diapause	after 21 d. at 30° C.	P
20	10	2.5	25	3.5	< 1 %
58	22	5.5	24.5	3.5	< 1 %
200	71	18	23.5	6.5	< 1 %
2,500	500	125	29	8	< 1 %
10,000	2,000	100	28	1	< 1 %

% positive choices

gradient (Lux)			in diapause	after 21 d. at 30° C.	P
20	10	2.5	48.5	58	10-20 %
58	22	5.5	59.5	79.5	< 1 %
200	71	18	50.5	56.5	20-30 %
2,500	500	125	45	60.5	< 1 %
10,000	2,000	500	67.5	79.5	5-10 %

high degree of humidity, the diapausing beetles were induced to emerge from the soil within 21 days (Fig. 4). At the end of this period we observed the formation of vitellinised eggs in the ovaries of many

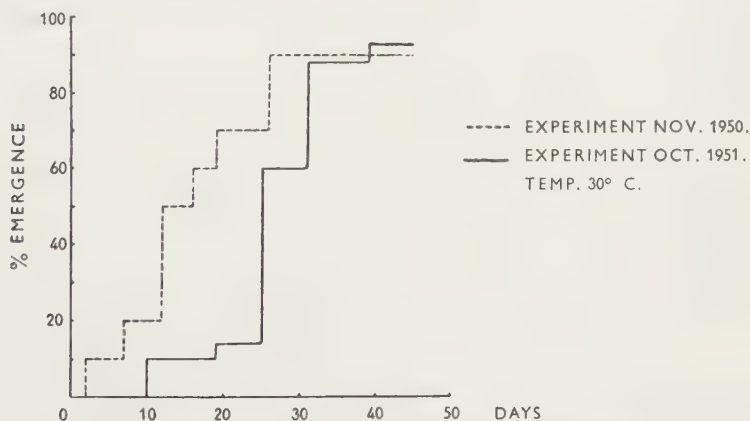


Fig. 4. Course of emergence from the soil after exposure to 30° C. and high humidity.

beetles (Fig. 5). If the treatment was prolonged and food was given, the animals would feed and oviposit within a short time.

IV. DIAPAUSE AND OVIPOSITION

Diapause and oviposition preclude each other. Factors which prevent diapause tend to increase egg formation. An outstanding example of

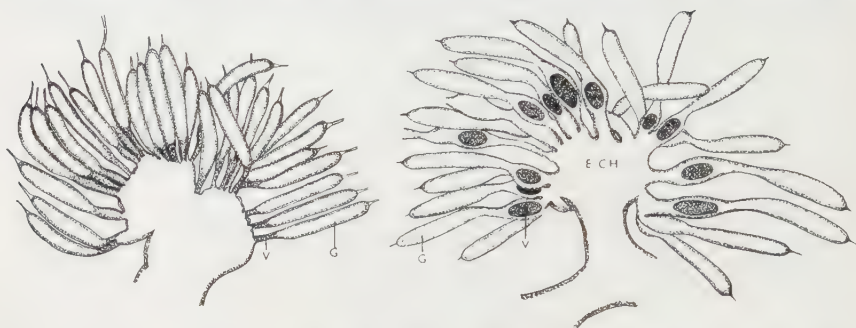


Fig. 5. Left: ovary of diapausing female. Right: Ovary of diapausing female placed at 30° C. during 14 days. G = germarium V = vitellarium E.CH = Egg chamber.

this was given during an experiment made in 1947 when 50 beetles were placed in a constant temperature room directly after the imaginal moult at a temperature of 28–29° C. and illuminated with cooled lamps at 3750 Lux during 24 hrs. p. d.

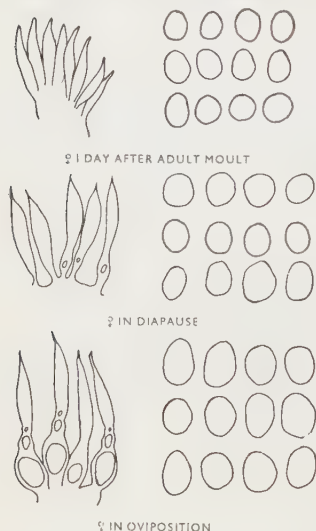


Fig. 7. Size of 12 corpora allata and development of the ovarioles in three stages of development of the adult beetle.

ovulation continues during diapause. The immature ova degenerate after some time, their contents seems to be resorbed by the egg follicle and the ovarian wall.

Another group of 50 beetles, belonging to the same culture as the first-named and emerged on the same day, was reared in the open. Both groups were fed on young leaves.

Only 50% of the first group entered into diapause, whereas 100% of the last group did so. In the 50%-group the females proceeded to lay eggs at a rate considerably higher than normal (Fig. 6).

Mature eggs can only be formed if the oocyte receives a sufficient amount of yolk. The bulk of this yolk is added to the ovum in the vitellarium of the ovarioles, whereas the oocytes are formed in the germarium. The ovarioles of *Leptinotarsa* belong, as in all Chrysomelids, to the telotrophic type.

Microscopical investigation showed that

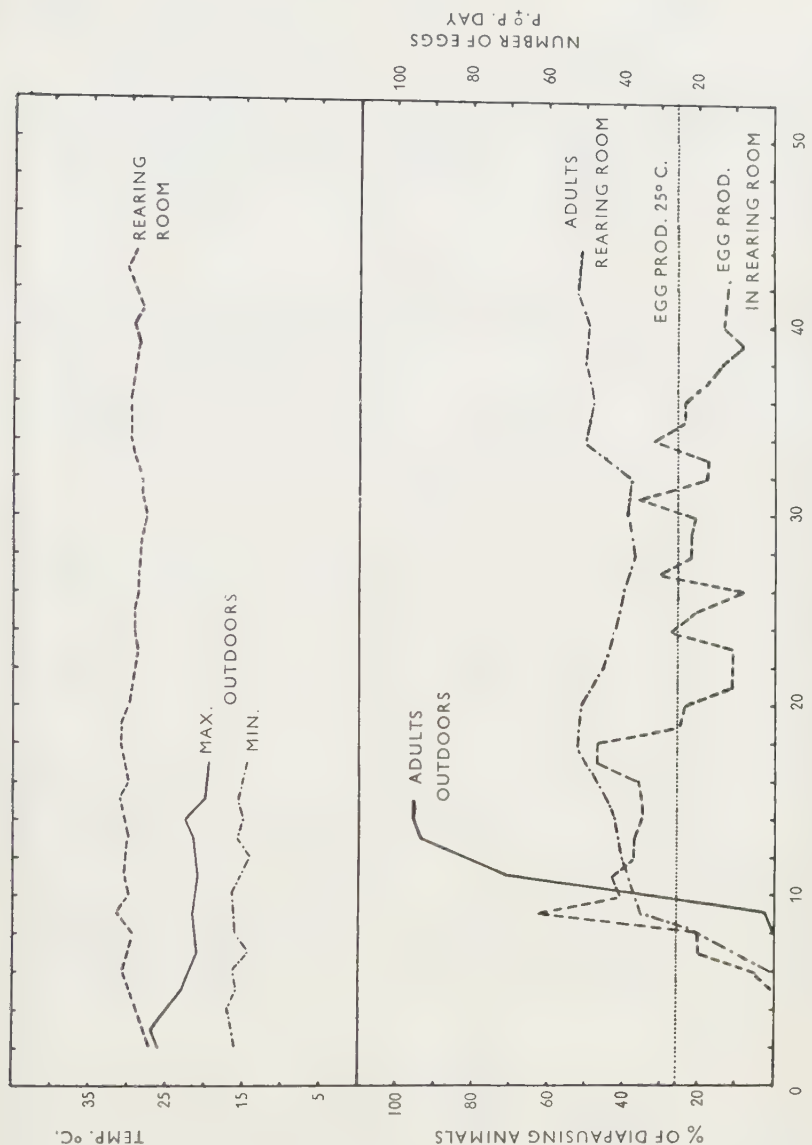


Fig. 6. Course of diapause and egg production in two groups of beetles, reared outdoors and in a rearing room. The horizontal line marks the normal level of egg production at 25° C.

According to several investigators (PFLUGFELDER 1937, WIGGLESWORTH 1937, JULY 1945, THOMSEN 1942) similar phenomena can be observed when the corpora allata are inactive or are extirpated. We have, therefore, studied the correlation between the vitellinisation of the eggs and the size of the corpora allata during adult development.

A positive correlation was found (Fig 7). We now presume that the absence of the corpora allata-hormone is the cause of the depressed ovogenesis during diapause.

Transplantation experiments are in course to decide on this matter. The function of the corpora allata, however, is known to depend on the cerebral ganglion. It remains an interesting problem whether the coordination centre, mentioned in our introduction, is present here.

SUMMARY

This paper briefly deals with the results of experiments on some characteristic elements of diapause in the adult Colorado-beetle, *Leptinotarsa decemlineata* Say.

It is argued that adult insects in diapause have some fundamental features in common with other diapausing stages, i.e.

1. Standstill of morphogenesis.
2. Strongly reduced basal metabolism.
3. Low water content, high fat content.

It is shown that increased water excretion, as mentioned by TOWER (1906), does not necessarily precede diapause.

During prediapause a gradual shift takes place in geotactic and phototactic behaviour. Geotaxis changes from negative to positive, the turning point being at the 10th day. Phototaxis only becomes less positive.

Diapause in *Leptinotarsa* is not broken by a stay at 5° C during 42 days. At 29–30° C and high humidity, all diapausing adults emerge within three weeks. Under these conditions, vitellinized eggs begin to develop in the ovarioles. Complete ova are only formed when regular food intake has begun.

The ovarioles of diapausing beetles resemble those of the Reduviid *Rhodnius* when the corpora allata are extirpated. During various stages of adult development, the size of the corpora allata correlates with the vitellinisation of the ova.

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THE POSTLARVAL DEVELOPMENT
OF THE PRONEPHROS IN
CHANOS CHANOS (Forsk.)

by

C. HOLSTVOOGD
(Amersfoort)

In the Amniota and Selachii the pronephros is a vestigial organ. The other fishes and the amphibia have a functional pronephros in the larval stage. This organ is formed early; the number of nephrons is thereby soon definitely fixed, so that the development into a functional organ is based on an increase in size, but never on an increase in the number of nephrons. Only in a relatively small number of Teleostei, mostly species of 3 to 4 inches, the pronephros remains permanently. It is formed by a single pair of nephrons which forms a cranial appendage of the rest of the kidney. The length of the tubules of the pronephric nephrons remains so small that the bloodpressure is sufficient to overcome the friction of the liquid in these tubules permanently.

In *Chanos chanos* or "bandeng" as it is called in Indonesia, however, we have quite different conditions. *Chanos* is a fish the size of a fair-sized cod, showing the remarkable phenomenon that the pronephros continues to develop after metamorphosis. Proximal to the opening of the first pair of mesonephric nephrons new nephrons continue to appear and this goes on as long as the animal is growing. The anatomical conditions in the cranial part of the kidney in *Chanos* are apparently of such a nature that all potentialities of the pronephros come to development.

Before proceeding to the description of the development of the kidney in *Chanos*, it is useful to make a distinction between nephrons and collecting ducts, though the boundaries between them are continually shifting in proximal direction. A nephron consists of a Malpighian body and a tubule, and the latter again has a proximal and a distal segment. The cells of the proximal segment have nuclei situated basally and a broad brush-border; those of the distal segment have nuclei situated cen-

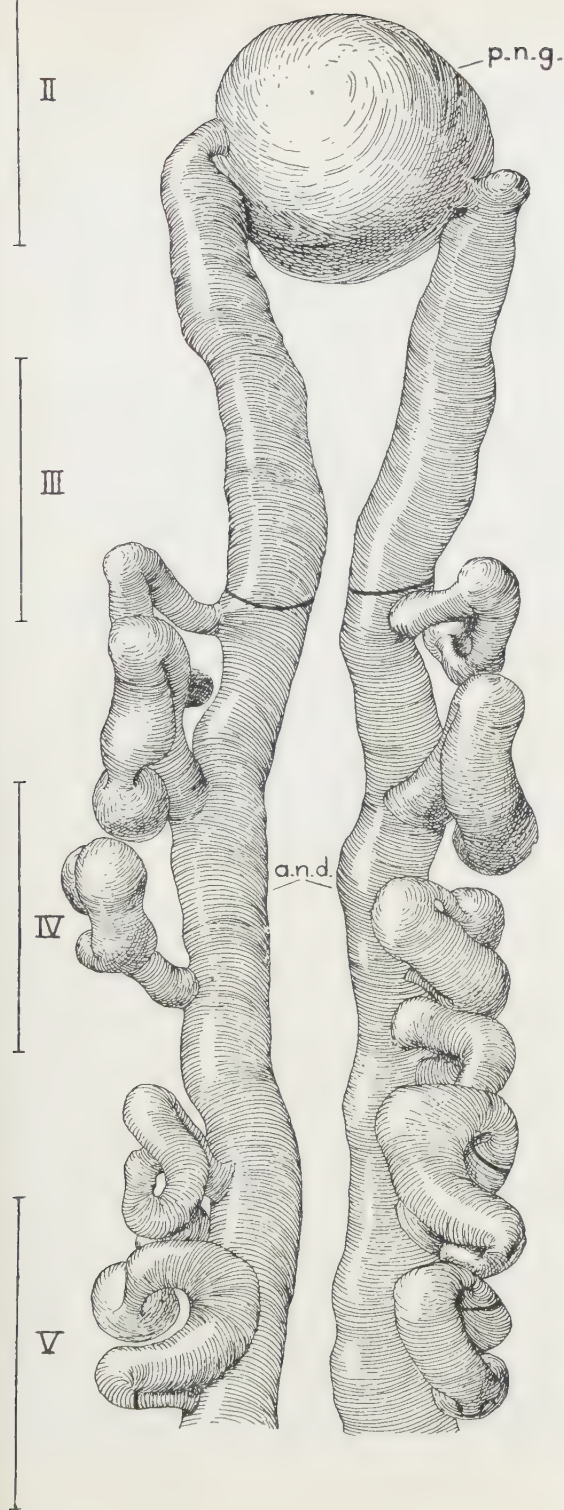


Fig. 1. *Chanos* 11 mm, reconstruction of anterior part of kidney, $\times 300$, ventral view. p.n.g. pronephric glomerulus, a.n.d. archinephric duct, II-V indication of the vertebrae 2-5 drawn next to the figure for the sake of clearness. The band across the tubules indicates boundary between proximal and distal epithelium.

trally and a narrow brush-border. For the rest, the picture shown by the cells of the proximal segment is fairly divergent, depending as it is on the fixation and functional condition.

When fixed in Romeis' fluid (ROMEIS, 1948) the protoplasm is much alveolated; when Bouin's fixative is used a layer of homogeneous protoplasm is seen beneath the brush-border, while in the rest of the protoplasm granules can often be found that strongly stain with eosine. When stained in Heidenhain's iron haematoxylin one sees numerous black inclusions in the protoplasm.

In newly hatched larvae (length 5 mm) the kidney consists of two nephrons, whose tubules run without coils in caudal direction. From position and bloodsupply of the glomerulus it appears that it is a typical pronephros, (HOLSTVOOGD, 1936).

In animals of 11 mm (fig. 1) an additional number of nephrons has developed. We call them secondary ones because they open externally via the first pair. The glomeruli of the two primary nephrons have fused just like their Bowman's capsules. Situated ventrally of the second vertebra, they are distinguished by their large dimensions. Blood is supplied directly by the aorta. The proximal epithelium runs uninterruptedly as far as the opening of the first secondary nephron, occasionally a little beyond it. On the dorsal side it may continue as far as the opening of the second nephron. The distal epithelium runs a little beyond the last secondary nephron, then it becomes flattened to pavement epithelium. The tubules of the secondary nephrons largely consist of proximal epithelium, only the junctional part has distal epithelium.

Fig. 2 shows a reconstruction of the anterior part of the kidney of a specimen (13 mm long) whose metamorphosis has just started. The large glomerulus has shifted in caudal direction over half a vertebra. As we demonstrated in 1936 this is connected with caudal shifting of the arteria epibranchiale IV and the arteria coeliaca. On the right the foremost secondary nephron still opens into the proximal segment of the primary tubule. Farther on another bit of proximal epithelium in each of these tubules is found. Joining the distal epithelium of the secondary nephrons, distal epithelium has apparently pushed itself in between the proximal epithelium. The tubules of the secondary nephrons have considerably lengthened, which fact is mainly due to the distal segment.

The animal from which the reconstruction, shown in fig. 3, has been derived, is somewhat shorter than the previous one, but more developed. The coils in the secondary nephrons have become less compact. The proximal segment of the tubules of the primary nephrons has formed large coils, but the glomerulus is still beneath the second

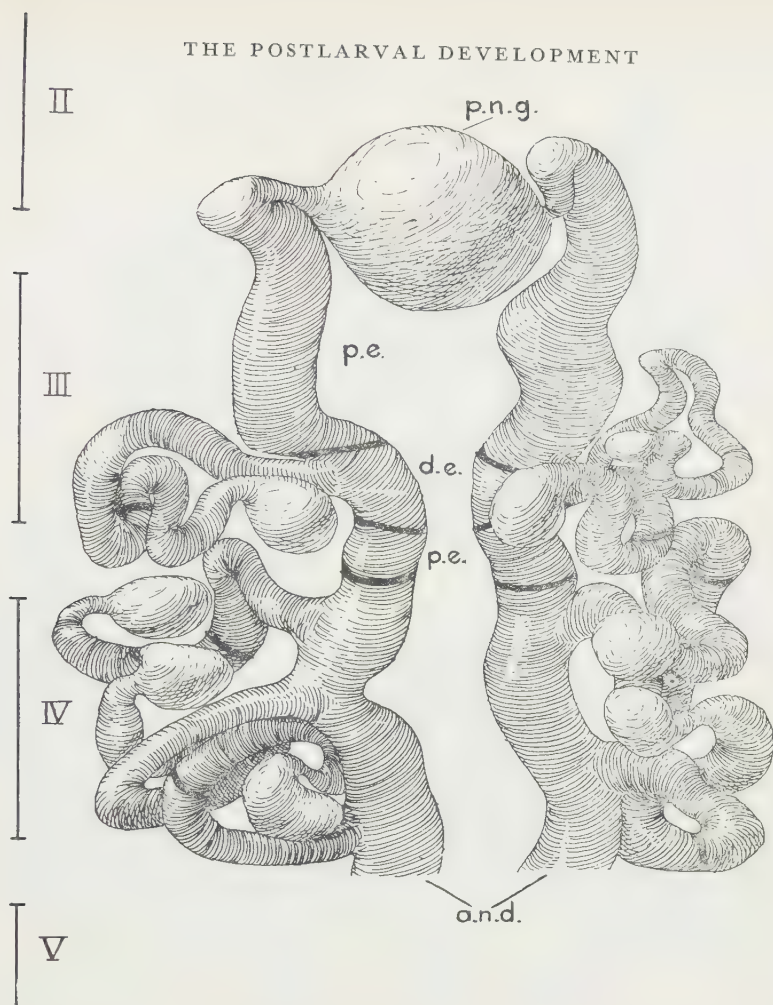


Fig. 2. *Chanos* 13 mm, reconstruction of anterior part of kidney, $\times 200$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. archinephric duct, II-V indication of vertebrae 2-5. The band across the tubules indicates boundary between proximal and distal epithelium, p.e. proximal epithelium, d.e. distal epithelium.

vertebra. For this reason the forming of these coils cannot be attributed to a shifting of the glomerules, but they develop in situ. The spreading of the two kinds of epithelium over the primary tubules is still fairly equal to that of the previous stage.

In a specimen of 12.7 mm (fig. 4) three kinds of epithelium can be observed on the primary tubules, namely: proximal epithelium, distal epithelium and epithelium typical of the collecting ducts. The latter is lower than the distal one and has homogeneous, dark-staining protoplasm. The cranial boundary of this collecting duct-epithelium

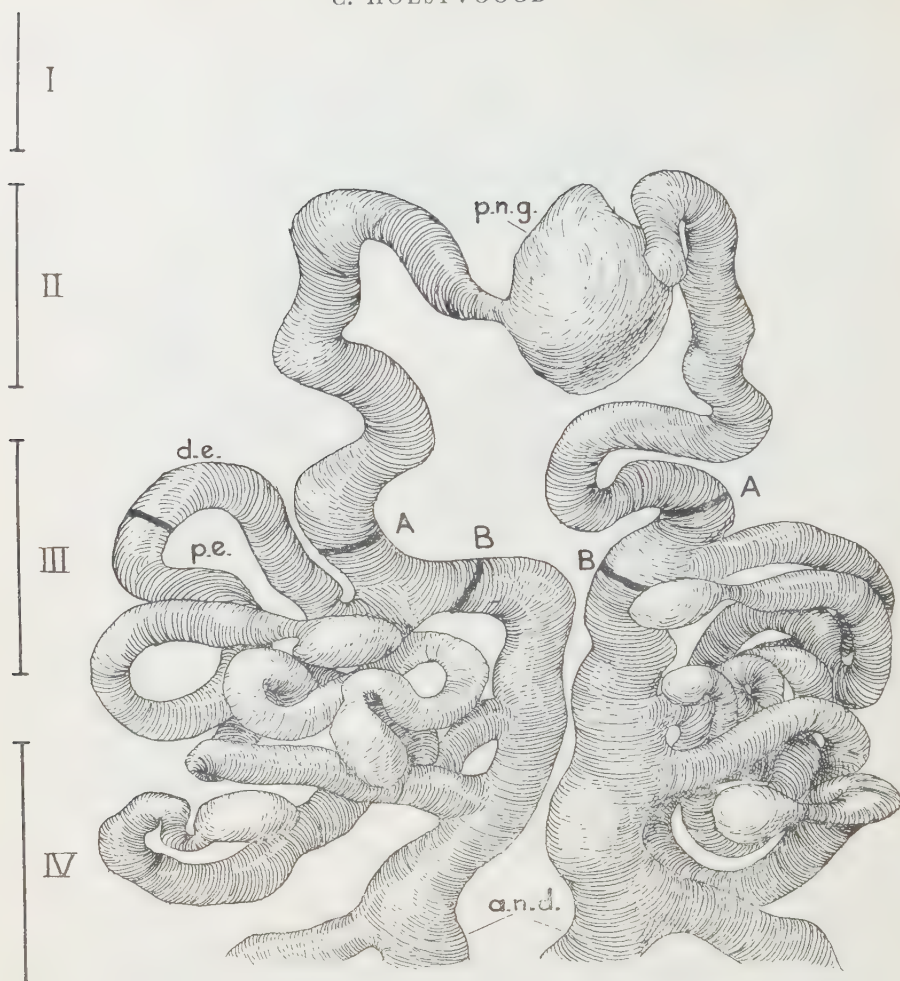


Fig. 3. *Chanos* 12 mm, reconstruction of anterior part of kidney, $\times 206$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. archinephric duct, p.e. proximal epithelium, d.e. distal epithelium. From A to B epithelium of which a number of cells still has the character of proximal epithelium. After B distal epithelium; II-IV indication of vertebrae.

is situated a little beyond the opening of the second secondary nephron. As will become more evident below, this boundary is continually shifting in proximal direction. The secondary nephrons partly stretched themselves. A backward and forward running loop can be observed in it. In so far as they open into the collecting duct their end sections also have collecting duct epithelium. The proximal segment of each of the primary tubules has also formed a backward and forward running loop. The large glomerulus is now at the level of the third

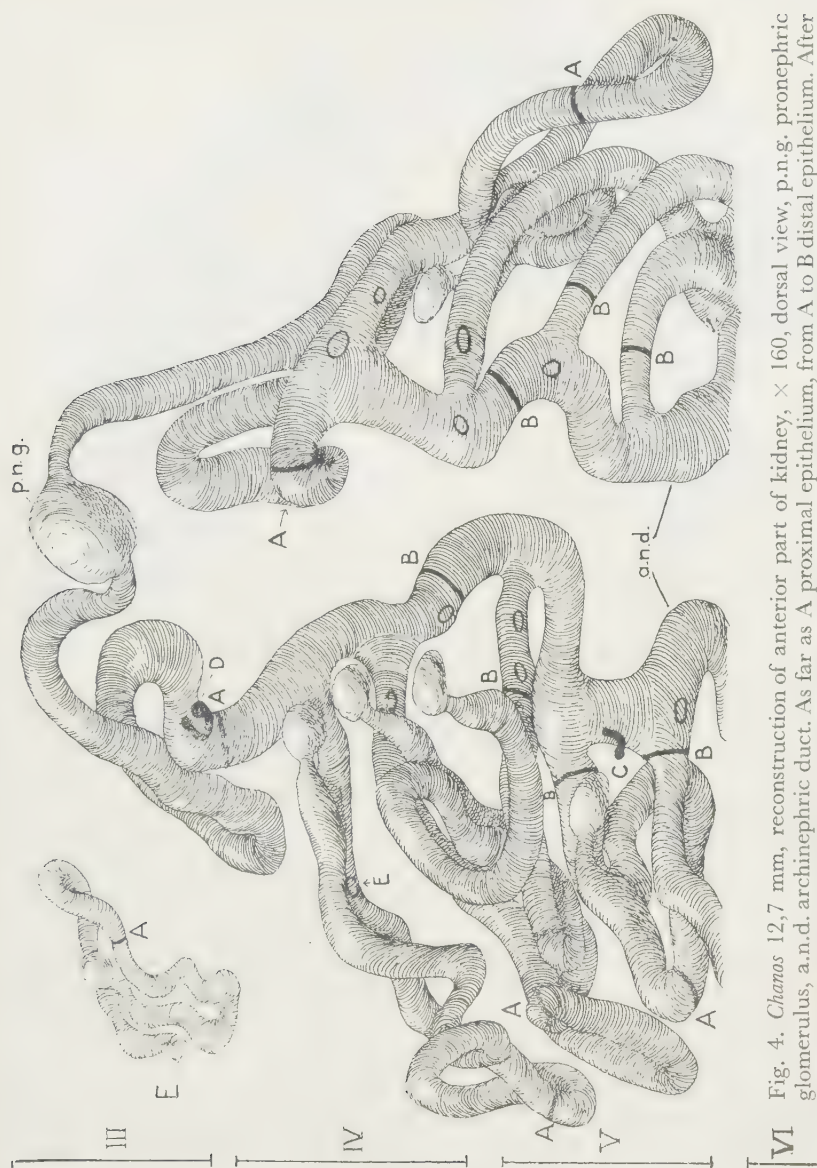


Fig. 4. *Chanas* 12,7 mm, reconstruction of anterior part of kidney, $\times 160$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. archinephric duct. As far as A proximal epithelium, from A to B distal epithelium. After B collecting duct epithelium. C young rudiment, D somewhat older. E place of opening of a young, but already functional nephron. The other ovals present the places of opening of the other young nephrons varying in development from C to E, III-V indication of vertebrae 3, 4 and 5.

vertebra. Several new nephrons are to be seen. Some of these function already, others are still in the knob- or elbowshaped stage. It is remarkable that also an "anlage" has arisen on the proximal segment of one of the primary tubules.

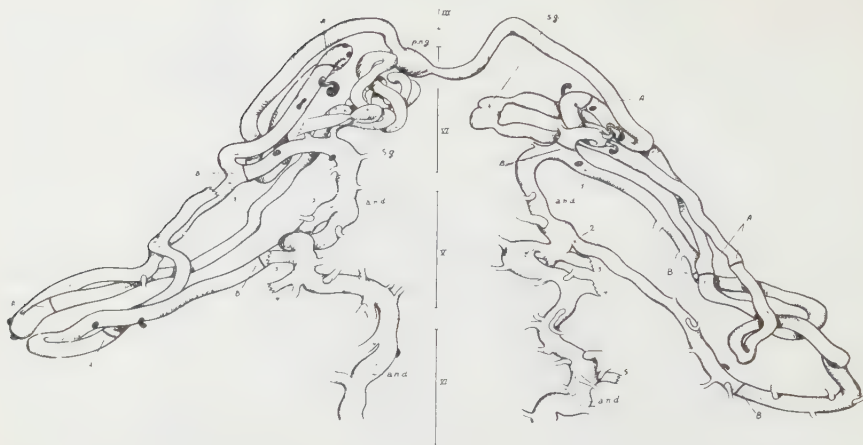


Fig. 5. *Chanos* 28 mm, reconstruction of anterior part of kidney. $\times 45$, dorsal view; p.n.g. pronephric glomerulus, a.n.d. archinephric duct, s.g. glomeruli of the two most anterior of the old secondary nephrons, on the right these glomeruli have fused. 1, 2, 3, 4, 5, openings of the old secondary nephrons in the archinephric duct. Furthermore there is a complete reconstruction of a young, but functional nephron; of the others only the opening is given. Rudiment of nephrons are drawn dark black. As far as A proximal epithelium, distal epithelium as far as B, after B collecting duct epithelium; III-VI indication of the vertebrae 3-6.

The reconstruction in fig. 5 presents a picture of the anterior part of the kidney of a *Chanos* specimen of 28 mm, with the restriction that of the younger nephrons only the openings have been indicated. An exception has been made for one of these nephrons; its tubule is a compact mass, just as in secondary nephrons in animals of 12 mm. Furthermore, to the left and to the right, two old secondary nephrons are drawn completely; they are conspicuous by their solid structure. An important part of the forward running loops has now attained the function of collecting ducts. Young rudiments are numerous; they are partly attached to the segments with proximal epithelium. The pronephric glomerulus is now situated beneath the anterior of the fourth vertebra.

So far the Malpighian bodies of the old secondary nephrons could be distinguished from the other ones by their large dimensions. In animals of 35 mm this is no longer the case. For this reason the reconstructions shown in figs. 6, 7 and 8 have been restricted to the primary nephrons. The pronephros glomerulus remains recognizable by its medial position at the radix of the arteria coeliaca (HOLSTVOOGD, 1936) and by its bloodsupply by means of a small artery originating ventrally from the aorta. The later formed glomeruli receive their blood from sidebranches of the aorta along which they are arranged

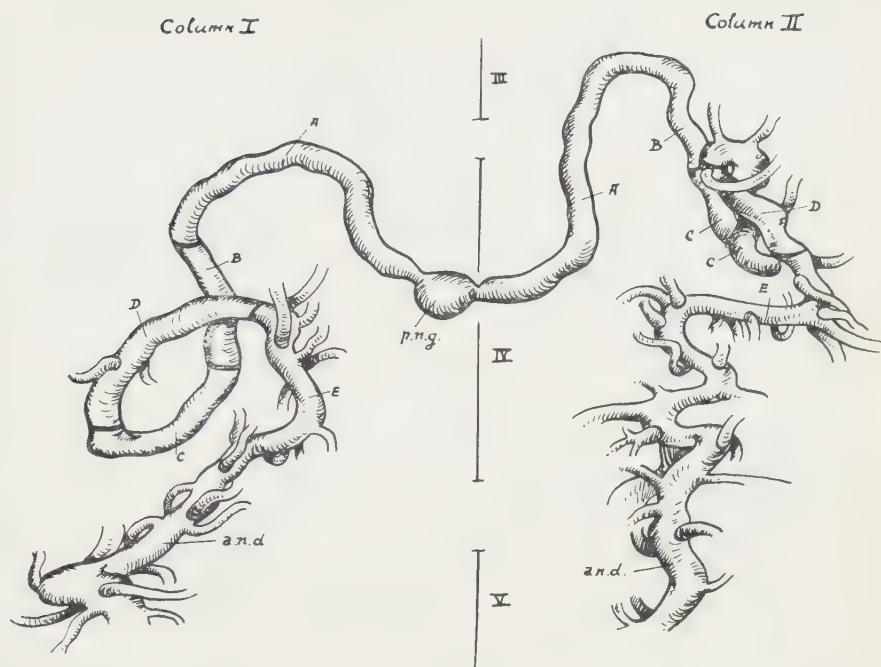


Fig. 6. *Chanos* 35 mm, reconstruction anterior part of kidney, $\times 92$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. archinephric duct, III–IV indication of vertebrae 3–5. See for letters A–E, table on page 395.

in clusters. Compared with the previous stage the pronephric glomerulus has again shifted in caudal direction, but the cranial boundary of the kidney has kept its old position, just as the loops in the primary tubules. One strongly gets the impression that the cranially running incipient part of each of these tubules has been newly formed. This impression is supported by the peculiar spreading of the kinds of epithelium out of which they are composed.

The way the different kinds of epithelium are spread over the primary tubules becomes clear when we assume that the elongation of these tubules is based on the growth of the part with proximal epithelium, whereby the earliest part again and again loses its function. At a certain moment the epithelium in this excretorily functionless part starts regenerating into distal epithelium.

Originally this new part is situated between two sections with proximal epithelium. In the animal from which the reconstruction of fig. 8 has been derived (column V and VI) this process has progressed so far that the distal part of the proximal epithelium (C) has lost its character as such. The right tubule of the animal of 35 mm (fig. 7,

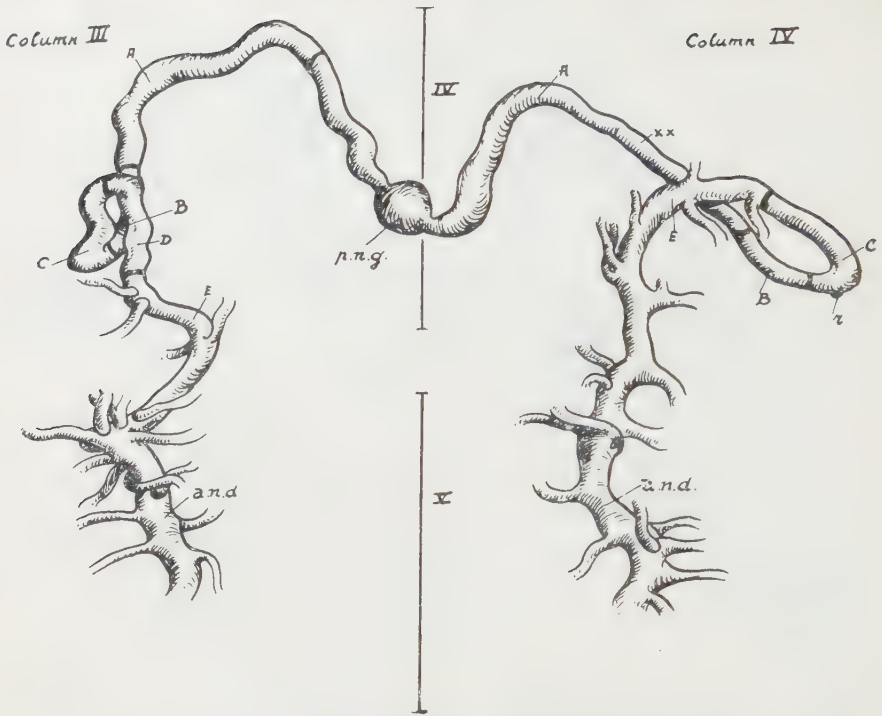


Fig. 7. *Chanos* 35 mm, reconstruction anterior part of kidney, $\times 92$, dorsal view, see for explanation fig. 6.

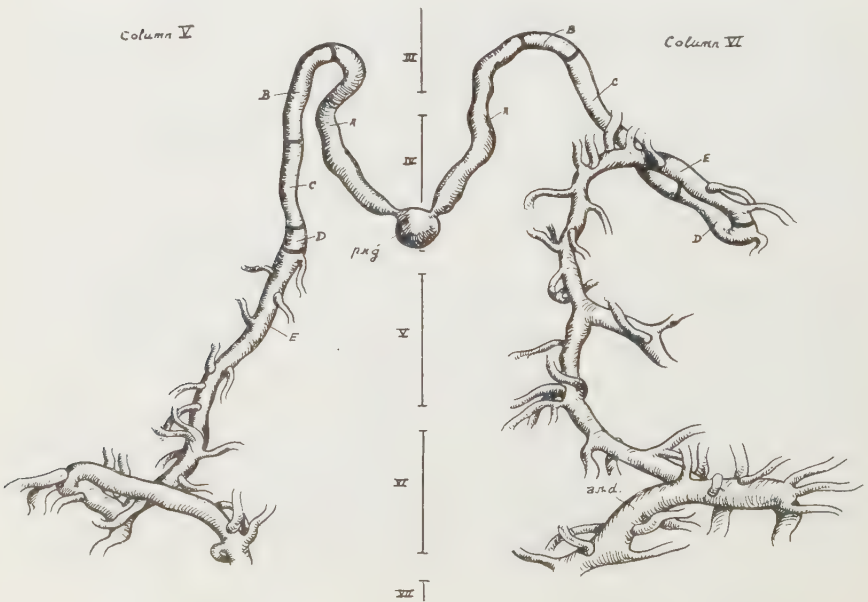


Fig. 8. *Chanos* 42 mm, reconstruction anterior part of kidney, $\times 65$, dorsal view. See fig. 6 for further explanation.

SURVEY OF THE KINDS OF EPITHELIUM
OUT OF WHICH THE INCIPIENT PARTS OF THE PRIMARY TUBULES
ARE FORMED IN ANIMALS OF 35, 35 AND 42 MM

35 mm, fig. 6

- | | |
|---|--|
| <p>I. A. proximal
B. basophilic
C. proximal
D. distal
E. collecting duct epithelium</p> | <p>II. A. proximal
B. basophilic
C. proximal
D. distal
E. collecting duct epithelium</p> |
|---|--|

35 mm, fig. 7

- | | |
|---|---|
| <p>III. A. proximal
B. basophilic

C. proximal

D. distal
E. collecting duct epithelium</p> | <p>IV. A. proximal
B. proximal; irregular, pale, homogeneous protoplasm
C. distal, with here and there dark nuclei

E. collecting duct epithelium</p> |
|---|---|

42 mm, fig. 8

- | | |
|---|--|
| <p>V. A. proximal
B. basophilic
C. irregular, greatly affected by lymphocytes
D. distal
E. collecting duct epithelium</p> | <p>VI. A. proximal
B. basophilic
C. irregular, affected by lymphocytes
D. distal
E. collecting duct epithelium</p> |
|---|--|

IV) has lagged behind. Part C is to be considered as the remnant of the previous renewal stage; presently, so we may picture it, somewhere near XX (fig. 7) basophilic epithelium will again appear as the beginning of the next epithelium regeneration.

The assumption that the growth of the tubule is brought about by the renewal of the proximal part is confirmed by what is found in an animal of 55 mm (fig. 9). The coils that join the glomerulus on the left must have been newly formed. The proximal and distal sections of the primary tubules, when compared with animals of 28 mm and younger, now consist of newly formed elements. The glomerulus is now but slightly larger than other twin-glomeruli, which are met with in the kidney here and there. The originally dominant pair of primary nephrons is reduced to a pair of common nephrons among many others.



Fig. 9. *Chanos* 55 mm, reconstruction anterior part of kidney, $\times 78$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. archinephric duct. As far as A proximal epithelium, from A to B distal epithelium, after B collecting duct epithelium, III-V indication of the vertebrae 3, 4 and 5. The dotted line indicates the anterior boundary of the kidney.

Fig. 10, 80 mm, shows the caudal outgrowth of the coils that join the pronephric glomerulus. A similar outgrowth occurred in the old secondary nephrons; see figs. 4 and 5. The course of the loops in the primary tubules appears to be rather variable, but in spite of that, in this animal we find them again in still clearly recognizable form.

In an animal of 250 mm (fig. 11) new nephrons are also originating again along the caudal outgrowth bordering the pronephric glomerulus. The youngest two have been reconstructed. The most proximal one is still in the S-shaped stage, while the other one has much farther



Fig. 10. *Chanos* 80 mm, reconstruction anterior part of kidney, $\times 44$ dorsal view, p.n.g. pronephric glomerulus a.n.d. archinephric duct. As far as A proximal epithelium, form A to B distal epithelium, B is followed by a part of irregular epithelium, which, after the first side-ducts, changes into the epithelium of the collecting ducts. IV-V indication of the vertebrae 4 and 5.

developed (compare fig. 5). As a variation of this stage we give a reconstruction of the initial part of the pronephros of an animal of 200 mm (fig. 12). In spite of the great difference in the course of the primary tubules, we also see much similarity; on the left the incipient part shows a caudal outgrowth, on the right we observe intricate coils. Throughout the entire kidney of this specimen, in the proximal epithelium of a considerable number of the nephrons, we find granules highly staining in eosine. They are likewise found in the proximal epithelium of the primary tubules. The excretorily active parts of the pronephros¹ differ in no respect from those of the other nephrons, except perhaps by a somewhat more solid structure (see photographs). In animals of 450 mm, the pronephric glomerulus, recognizable by its characteristic position and bloodsupply could easily be found again.

When *Chanos* has reached the length of about 900 mm it is mature. These animals are hard to obtain in fresh condition. Externally the

¹ Viz. the glomerulus and the proximal and distal sections of the primary tubules.



Fig. 11. *Chanos* 250 mm, reconstruction anterior part of kidney, $\times 27.5$, dorsal view, p.n.g. pronephric glomerulus, a.n.d. pronephric duct, r. rudiment of a still basophilic nephron, j.n. young nephron already functional. Proximal epithelium as far as A, from A to B distal epithelium, after that comes a part of irregular epithelium, acquiring the character of the epithelium of collecting ducts at the first openings.

kidney of these animals does not differ from those of 250 mm (figs. 13a, 13b). Naturally the sections of the anterior part of the kidney fixed about 6 hours post mortem were not perfect; yet it could be ascertained that tubules and Malpighian bodies occurred as far as the most anterior end. In addition to the animals discussed in this paper, a larger number has been investigated more superficially; from them it appeared that the primary glomerulus sometimes gets an asymmetrical position, so that one primary tubule has to pass underneath the aorta. In some cases only one tubule was left.

Finally, the results of our investigation have to fit in with the present knowledge of the structure and development of the kidney of the Vertebrata. No easy task, as reports on a persistent pronephros in fishes have often met with a certain suspicion and vexation. When BALFOUR happened to come across ROSENBERG's publication (1867),

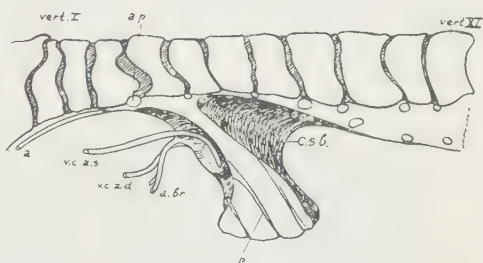
Fig. 12. *Chanos* 200 mm, reconstruction of a part of kidney, $\times 60$, p.n.g. pronephric glomerulus, a.n.d. archinephric duct, m.l°.n. opening of the most proximal nephron. Proximal epithelium as far as A, from A to B distal epithelium, after B the epithelium of the collecting ducts. The dotted line indicates the cranial boundary of the kidney.



Fig. 13a. Kidney of a *Chanos* of 250 mm, $\times \frac{1}{2}$, a. aorta, a.br. art. epibranchiale, v.c.a. vena card. post., a.m.a. art. coeliaca + art. mesenterica ant., a.m.p. art. mesenterica post., u.b. urine bladder.



Fig. 13b. Anterior part of the kidney of a *Chanos* of 980 mm, $\times \frac{1}{2}$, vert. I first vertebra, vert. XI eleventh vertebra, a.p. pectoral art., a. aorta, v.c.a.s. left vena card. ant., v.c.a.d. right vena card. ant., a. br. epibranchial art., r. impressions of ribs; v.s.b. cavity filled in by an outgrowth of the swimming bladder. The pronephric region of the kidney lies ventrally from the vertebrae 3, 4 and 5.



in which the latter put the headkidney (HYRTL, 1851) on a par with the pronephros, he took the trouble to examine the kidneys of *Esox lucius*, *Osmerus eperlanus*, and *Anquilla anguilla*, but in the cranial region of the kidney of these fishes he found only lymphoid tissue.

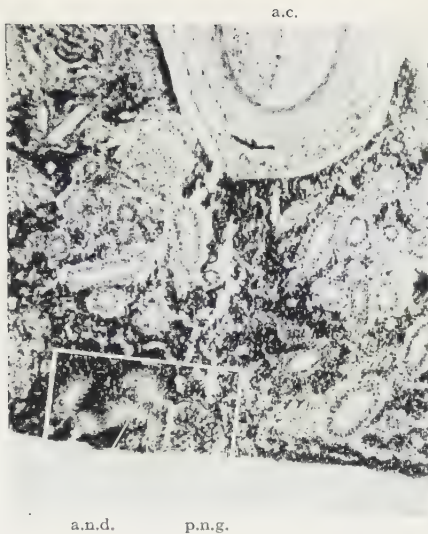
In November 1881 and January 1882 he reported on his investigation" and he concluded: "As the question at present stands, it appears to me that the probabilities are in favour of there being no functionally active remains of the pronephros in adult Teleostei, and that in any case the burden of the proof rests with those who maintain that such remnants are to be found." Now it is remarkable that in December 1881, EMERY made a communication about the occurrence of a functional pronephros in the mature *Fierasfer*, and the next year (1882) he was able to give *Zoarces* as a second example of a persistent pronephros. EMERY's report made little impression, and when in 1883 PARKER, who after BALFOUR's death continued his work, lectured on the kidneys of fishes, no mention was made of EMERY's findings at all. GROSLIK (1885) was more positive about EMERY's work. GROSLIK also investigated the kidneys of a number of bony fishes (*Cyprinus carpio*, *Esox lucius*, *Rhodeus amarus*, *Gasterosteus aculeatus*) but no more than BALFOUR did he find any trace of a pronephros in adult animals. According to GROSLIK, EMERY must have worked with material not yet fully developed.

History repeated itself with the fine investigations of GUITEL (1903, 1905, 1908). AUDIGÉ (1910) did not find a single species with a persistent pronephros in his extensive material and he is sceptical about GUITEL's results. In 1932 PADOVANI examined the kidneys of *Zoarces viviparus*, *Gobius minutus*, *Hippocampus brevisrostris*, and *Syngnathus acus* but, unlike EMERY and GUITEL, did not meet with a persistent pronephros. In 1936 the present author found a persistent pronephros in *Dermogenys pusillus*, while in 1941 GÉRARD could confirm GUITEL's results in *Cottus gobio*, and was able to add two other examples to the list, now comprising about 20 species.

What then can be the reason of the sceptical attitude towards communications on the occurrence of a persistent pronephros in Teleostei? It leads sometimes to the following strange syllogism (GROSLIK, 1885): *Fierasfer* has no permanent pronephros, since carp, pike, stickleback and tri on have none. An answer to this question will be obtained by paying attention to the theoretical consideration this sceptical attitude arises from.

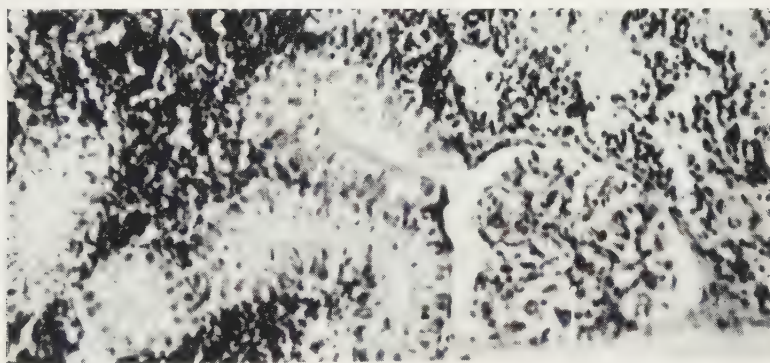
"Dans l'ontogénie comme dans série ascendante des Vertèbres le développement (des reins) se fait dans le sens cranio-caudal et que c'est la région la plus caudale qui reste seule fonctionnelle" (PADOVANI, 1932).

Are some Teleostei an exception to this rule?



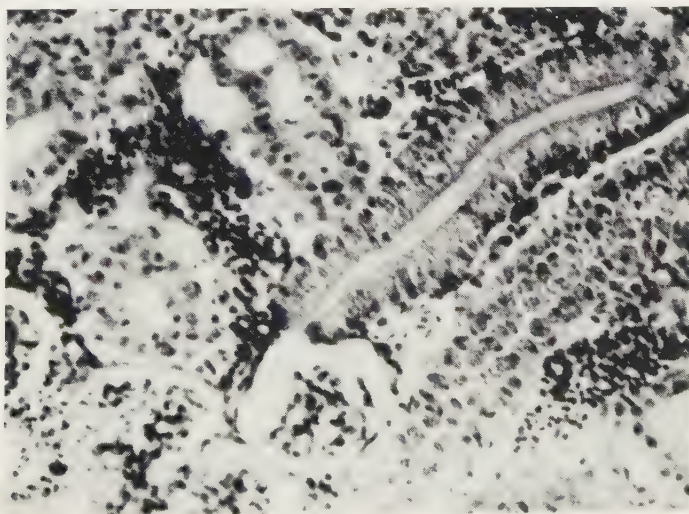
a.n.d. p.n.g.

Photograph *a*. cross section through C of Fig. 12, $\times 96$; a.c. art. coeliaca, p.n.g. pronephric glomerulus, a.n.d. archinephric duct.



p.n.g.

Photograph *b*. the outlined part in photograph *a*, $\times 384$, p.n.g. pronephric glomerulus.



Photograph *c*. a cluster of ordinary glomeruli from the same section.

If we want to compare the theories on the development of kidneys of the Vertebrata with the results of our investigation, it will be necessary to go into it somewhat more extensively; in this we follow IHLE's summary (1924). According to RÜCKERT the kidney of the Vertebrata must be derived from a series of segmental excretory tubules that originally stretched up to the posterior end of the trunk. The anterior part maintained its original character and became pronephros, but in the more posterior end the tubules were reduced and replaced by newly developed ones, thus forming the "anlage" of the mesonephros. RÜCKERT considered pronephros and mesonephros as two different organs which phylogenetically originated one after another. This conclusion is not confirmed by the results in *Chanos*. Pro- and mesonephros are parts of one organ which can only be told apart with difficulty. Also according to BALFOUR and to SECKGWIK the primitive Vertebrata had an excretory organ that stretched over the entire length of the trunk. It differentiated into 2 or 3 parts situated the one behind the other and gradually merging into each other. According to these authors pro- and mesonephric tubules are primary ones, which are serially homologous: pro- and mesonephros are parts of the same organ, the holonephros. The findings in *Chanos* confirm this final conclusion but not the presuppositions it is based on. In *Chanos* the pronephric nephrons are the primae inter paris, which go through all the adventures of the secondary nephrons, those of the mesonephros, but nevertheless remain primary. The development of the kidney of *Chanos* reminds one of the growth of a plant. At first there is only a germ-plant with two leaves (pronephros). Later on side-branches (mesonephros) develop and while these are branching off in their turn, new side-branches continue to develop on the stem itself.

Just as the structure of the young stem goes on changing, so does the epithelium of the nephrons. That which first consisted of proximal epithelium, has distal epithelium later on, and still later on the epithelium of the collecting ducts. The entire development of the kidney in *Chanos* can be seen as the development of one single pair of nephrons, the pronephros.

BURLEND (1931) derived the kidney from a pair of folds in the somatopleura that have taken over the function of the coelome as excretory organ. These folds closed into two ducts, while here and there communications with isolated parts of the coelome remained. The isolated parts of the coelome developed into glomeruli, the communications into tubules, which from the very first need therefore not have been arranged segmentally, though they are so now by the segmental arrangement of spinal-nerves, myotomes, etc. Thus BURLEND was of opinion that the way in which the kidney arises in Myxinoidea, Teleo-

stei, Dipnoi, and Amphibia (Apoda excepted), is typical, whereas according to the older theories this way of originating has to be considered as atypical. According to BURLEND investigators were too much influenced by the way the kidney originated in Gymnophiona (BRAUER, 1902) and some Selachii, a.o. *Acanthias* (BORCEA, 1906). In BURLEND's view it is incorrect to think a way of origin atypical when it is exactly that way which leads to a good functional organ. If one wants to take a primordial form of the Vertebrata as a starting point, it is to be expected that more of the original condition has been left in the lower Vertebrata than in the higher ones.

The tubules of the primary nephrons that run without coils in caudal direction, represent the archinephric ducts, to which the glomeruli are joined as isolated parts of the coelome. According to this theory these tubules consist largely of proximal and distal epithelium. The same condition is found in young specimens of *Elops*, *Megalops* and *Chirocentrus* (HOLSTVOOGD, 1936). According to KINDAHL (1937) the cranial part of the archinephric duct in *Protopterus*, *Neoceratodus*, and *Triton* is formed by proximal epithelium.

The absence of pronephric tubules, in the sense of the older theories, is according to BURLEND's theory a primitive condition and needs no further explanation.

According to the older theories the development of the archinephric ducts, as presented by figs. 3-12, is a curious anomaly but it confirms BURLEND's view, for the archinephric ducts together with the glomeruli form the primitive excretory organ and these two nephrons are distinguished only from those that originate later by being the first. Experimental embryological investigation has confirmed the leading part of the archinephric duct plays in the development of the kidney. In *Amblystoma punctatum* the archinephric duct develops independently of the rest of the pronephros, as was demonstrated by VAN DETH (1946). CAMBAR (1947) showed that after displacement of a part of the archinephric duct and extirpation of the rest, the mesonephros only develops well opposite the displaced part.

About four fifths of the work necessary for the publication of this paper was carried out in Indonesia during the years 1936-1939; it was interrupted by the war. The rest of the sections was prepared in the Department of Prop. Zoology in Amsterdam. My colleagues MR H. J. HAANTJES and MR K. PIJLMAN converted my reconstructions into attractive figures. After my repatriation DR J. D. F. HARDENBERG, director of the Laboratory for Marine Investigations at Djakarta, kindly supplied me with some material.

SUMMARY

The development of the pronephros of *Chanos chanos* is described as it occurs after metamorphosis. Anyhow the growth of the pronephros continues until the animal has reached a length of 450 mm, but it is probable that the development goes on as long as the animal itself increases in length. During this development the pronephric nephrons sustain all changes that take place also in the mesonephric nephrons. Thus the pronephros of *Chanos* has quite a different character from the ones which have so far been described in literature. When finally the theories on the derivation of kidneys of vertebrates are surveyed, it appears that the results obtained tally best with those of BURLAND.

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HYDROGRAPHY OF THE DUTCH WADDEN SEA

A STUDY OF THE RELATIONS BETWEEN WATER MOVEMENT,
THE TRANSPORT OF SUSPENDED
MATERIALS AND THE PRODUCTION OF ORGANIC MATTER

by

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I. INTRODUCTION

I. DEVELOPMENT AND PURPOSE OF THE INVESTIGATION

This paper is concerned with the hydrography of part of the Dutch Wadden Sea. During recent years coastal waters and more especially estuaries have received much attention. One reason is the increased economic and social importance of these areas, which made a better knowledge of their hydrographic conditions desirable; the other reason is the advance of marine science, which contributed to an increased theoretical interest in estuarine problems.

The present investigation has been stimulated by biological work carried out by the Zoological Station at Den Helder. The chief line of research of this institution is the ecology of marine animals, which requires a profound knowledge of their environment. Bottom structure, tidal movements, temperature and salinity are among the outstanding factors regulating the distribution of these animals; the availability of organic matter and, indirectly, of nutrient salts, determines their potential growth.

Therefore, many data about these hydrographical elements (including bottom structure) have been collected over a number of years. A study of water movement and the distribution of salinity and temperature has already been published (POSTMA and VERWEY, 1950; POSTMA, 1950). The seasonal variation of nutrients in the harbour of Den Helder was studied by SCHEELE and VERWEY (unpublished). The composition of suspended matter has been analysed by SCHEELE at the request of the "Rijkswaterstaat", who were interested in this subject for reasons of land reclamation.

There is a close interrelation between the above-mentioned subjects, which makes it difficult to study them separately and renders it valuable to discuss them as a whole. Above all, knowledge of water movement is fundamental. Without this knowledge it is impossible to study matters of transport, to understand the reason for the actual composition of suspended matter, and to investigate the cycle of nutrients. Moreover, a study of nutrients must remain incomplete, if we do not consider how they affect the suspended organic material.

The above subjects will therefore be discussed here simultaneously, and stress will be laid on their interdependence. Chapter II is concerned with *water movement*, chapter III with the *transport and distribution of suspended matter*, and chapter IV with the *seasonal cycle of nutrients and organic matter*.

1. In studying *water movement*, the exchange of water between the

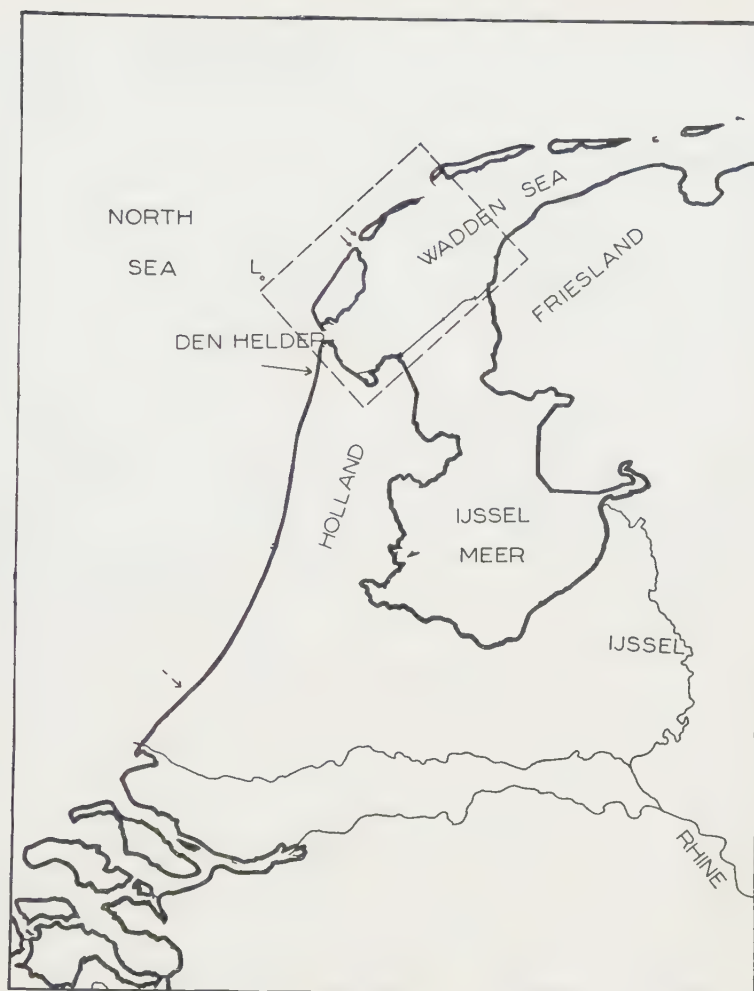


Fig. 1. Location of the area investigated, indicated by the rectangle; the arrows in the North Sea refer to the position and length of the sections of Table 13. L indicates the position of the lightvessel Texel.

Wadden Sea and the open North Sea will be emphasized. The concentration within the Wadden Sea of some substance or other (e.g. a nutrient or river water) depends on the rate of supply of this substance from, for instance, the main land, and the rate of exchange between the Wadden Sea and the North Sea. The greater this exchange, the more important will be the influence of the North Sea on the Wadden Sea. An attempt will be made to find a quantitative measure for this rate of exchange.

2. As regards *suspended matter*, superficial observations already show that the water of this region is very turbid. This becomes especially clear when the area is compared with the open North Sea. In the Wadden Sea a white disc, lowered into the water, is only visible to a depth varying between 0.5 and 5 meters, whereas the visibility in the North Sea mostly extends to ten meters or more. Exact measurements in many different parts of the Dutch, German and Danish Wadden Sea have confirmed that large quantities of material are present in suspension. In chapter III an attempt will be made to explain the presence of these large quantities of suspended matter. In this connection knowledge of the water exchange between Wadden Sea and North Sea is indispensable.

3. As part of the suspended material the *organic matter* is naturally subject to the same laws of transport as the suspension itself. The cycle of nutrient salts and the production of organic matter will be discussed in chapter IV. It will appear that a distinction must be made between the production of organic matter within the Wadden Sea itself, and the exchange of organic matter and nutrients between the Wadden Sea and North Sea. It goes without saying that here again knowledge

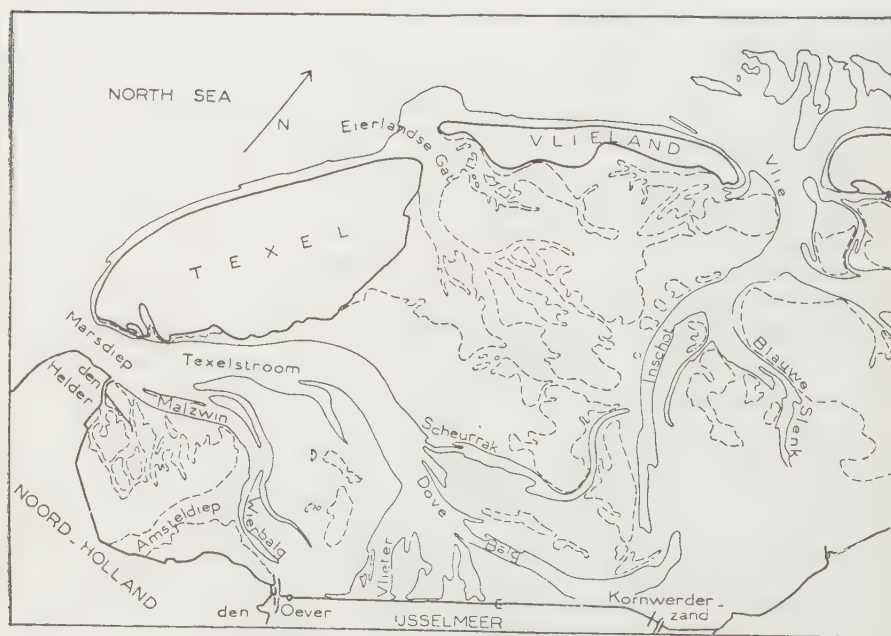


Fig. 2. Map of the western part of the Dutch Wadden Sea; intertidal flats are enclosed by dotted lines of Mean Low Water.

of the rate of water exchange is of primary importance. Of the various nutrients especially phosphorus was studied in detail.

I owe many thanks to Dr. J. VERWEY, director of the Zoological Station, for his stimulating interest taken in my work and his valuable advice. Thanks are also due to Prof. Dr. G. P. BAERENDS for his critical reading of the manuscript. The analyses of the large numbers of samples would not have been possible without the assistance of Miss E. GROEN, Mr. N. PIJL and Mr. A. DRAL. The manuscript and the tables were typed carefully by Miss T. STOLL. To Mr. J. SPIEKERMAN, den Helder, I am greatly indebted for his thorough correction of the English text.

2. DESCRIPTION OF THE AREA INVESTIGATED

Viewed as a whole the Wadden Sea is an oblong coastal sea, on one side bounded by the continental coast, on the other separated from the North Sea by a chain of islands. Its total length from Den Helder, Holland, to Esbjerg, Denmark, amounts to several hundreds of kilometers, whereas the distance between the coast and the islands is only some dozens of kilometers.

Between the islands several tidal inlets form the connection with the North Sea. Every inlet supplies a small region of the Wadden Sea with water. From the point of view of water movement every area is well separated from its neighbours and can therefore be considered an independent unit. As the areas are similar in many respects conclusions gained from research in one of them can often be applied to the others.

In every area the tidal inflow and removal of water takes place through a rather complicated system of tidal channels and creeks. Going inward the channels decrease in capacity until they gradually merge into large tidal flats (Wadden).

Many parts of the Wadden Sea receive fresh water from the mainland, some of them in large, others in small or even insignificant quantities. Generally speaking, the salinity of the Wadden Sea is therefore considerably lower than of the North Sea.

The investigations here dealt with were chiefly carried out in the westernmost part of the area. This part is connected with the North Sea by the tidal inlet of Den Helder (Marsdiep, figs. 1 and 2). Up to 1931 the Zuiderzee – as it still was then – was connected with this area by a broad open expanse of flats and channels, through which all water flowing into and leaving the Zuiderzee under influence of the tides passed. The course of the channels reminds us even at the present day of that state of affairs. In 1931 the Zuiderzee was closed off by a

heavy dike, the "Afsluitdijk", which turned it into the "IJsselmeer". The Afsluitdijk thus forms the boundary of the area under discussion.

Fresh water from the IJsselmeer enters the Wadden Sea at low tide through two sets of sluices, situated at either end of the Afsluitdijk near Den Oever and Kornwerderzand. The IJsselmeer in its turn

TABLE I
Numerical data of the Marsdiep area; compare fig. 2.

1. Total area covered	$0.69 \times 10^9 \text{ m}^2$
2. Dry at mean low water (M.L.W.)	$0.15 \times 10^9 \text{ m}^2$
3. Average depth at mean sea level (M.S.L.)	3.9 m
4. Water volume at M.S.L.	$2.7 \times 10^9 \text{ m}^3$
5. Average tidal amplitude at Den Helder.	1.35 m
6. Water volume at mean high water (M.H.W.)	$3.1 \times 10^9 \text{ m}^3$
7. Water volume at M.L.W.	$2.2 \times 10^9 \text{ m}^3$
8. Water volume entering the area through the Marsdiep with the flood and leaving with the ebb.	$0.93 \times 10^9 \text{ m}^3$
9. Average discharge per tide of fresh water from the IJsselmeer (1949, 1950, 1951)	$16.8 \times 10^6 \text{ m}^3$
10. Fresh water discharged at Den Oever	$10.3 \times 10^6 \text{ m}^3$
11. Fresh water discharged at Kornwerderzand	$6.5 \times 10^6 \text{ m}^3$
12. Average discharge per tide of fresh water at Den Helder	$0.8 \times 10^6 \text{ m}^3$

Remarks: 1, 2, 3: derived from a chart of the Dutch Hydrographic Office; 5: from tables of the Rijkswaterstaat; 9: unpublished measurements of the Rijkswaterstaat; 10, 11: data from the Dienst Zuiderzeewerken; 12: data from the Provinciale Waterstaat van Noord Holland.

receives most of its fresh water from the IJssel, a distributary of the Rhine. Smaller quantities of fresh water reach the Wadden Sea through locks near Den Helder and at two points on the Frisian coast. Numerical data about the tidal movements and volumes of water are given in table I. The transport of water under influence of the tide is very considerable; as compared with the total quantity present in the area, the supply of fresh water is comparatively small. The area is on the average very shallow, although depths up to 30–50 m occur in the tidal inlets.

The bottom of the larger part of the area consists of sand; mud is only found in sheltered places, for example on tidal flats near the coast and in some dammed-up channels, compare p. 473.

3. SAMPLING AND ANALYSES

Several thousands of water samples have been taken over the whole area of investigation, the larger part of them between Den Helder and Den Oever.

Generally speaking, surface samples were taken with a galvanised

iron bucket. In the case of samples to be analysed for suspended matter a special water bottle was used (see below), because when a bucket is used particulate matter easily sinks down before the water is transferred to a bottle.

Surface temperature was determined immediately after sampling with a frameless and verified thermometer divided into tenths of centigrades. Reading was accurate up to about 0.03°C ; for series of observations the relative accuracy was about 0.02°C .

For subsurface samples, except for those to be analysed on suspended matter, the well-known Nansen reversing water bottle with reversing thermometers was used; the temperature readings are accurate up to about 0.01°C . Samples for determining the quantity of suspended matter were obtained with a simple water sampler of our own design (fig. 3), by means of which the sample bottles, lowered into the water, were filled on the spot.

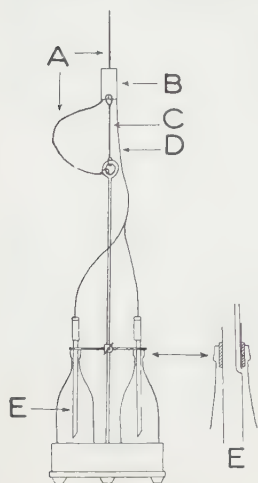


Fig. 3. Sampler for suspended matter.

This sampler for particulate matter works as follows. It is lowered into the sea on a steel wire (A), which is provided with a tripping mechanism (B). By means of a so-called messenger, lowered along the steel wire, a short rope (C), connecting the sampling apparatus (E) with B, is released from B. E drops down until the slack lower loop of A is taut. The drop stretches a third line D connecting B with the rubber hoods closing the bottles, so that the hoods are torn off. Water flows into the bottles through a long and wide tube, and the air escapes through a short narrow one; the filling of the bottle requires only a few seconds. When being pulled up, the instrument is not closed; nevertheless, no appreciable quantity of suspended matter "rains" into the bottles during that period.

The instrument functions properly at least to a depth of about a hundred fathoms. The samples were analysed in the laboratory. The various processes of determinations will be discussed hereafter. Special attention will only be given to some newly developed or modified methods.

A. Salinity (Chlorinity)

A. *Salinity* (Chlorinity) was determined according to the wellknown MOHR-KNUDSEN method for sea water, modified by VAN DAM (1940). In this modification the KNUDSEN pipette of 15 cm^3 was replaced by VAN DAM's micropipette with a volume of about 1 cm^3 . The silvernitrate solution was diluted accordingly.

The procedure has the advantage of being faster than the standard one without being less accurate. Accuracy has been maintained by using potassium chromate in the same quantity as in the standard procedure. This means a higher concentration of chromate at the end

point of the titration, the volume being only half as large. Therefore, the solubility product of silver chromate is easily attained after the precipitation of chloride has been completed. Moreover, at the end point of the titration the quantity of silver chloride is much smaller than is the case in the standard method; the delay of colour change caused by absorption of chloride ions at the precipitate is therefore probably shorter.

B. Suspended matter

a. *Quantitative determination.* Suspended matter was separated from the water by filtration under suction. Ash-free filter discs with a diameter of 5 cm and of normal gradation (SCHLEICHER and SCHÜLL, nr. 589) were used. Compared with very fine-grade filterpaper 3% at the utmost of the suspended matter was lost in passing through the filter. This was considered to be a negligible quantity. A greater loss occurs in fresh water, so that fine-graded filter paper had to be used here. In this case the filtration of one litre of water sometimes took many hours; the same volume of seawater is easily filtered within a quarter of an hour. Since very many samples had to be analysed rapid filtration was essential and a small loss of suspended matter had to be accepted.

The dry weight of the suspended matter was determined as follows. Before use the filter discs were dried at 110–120° C and weighed. The hygroscopy of the filter paper necessitated precautions against a gain in weight, by weighing in a closed glass vial. After filtration the discs were cleared of salt with fresh water, dried at 110–120° for more than 3 hours, and weighed again. The results are reliable up to about 1 mg/l. The accuracy of the method was checked regularly.

Before filtration, the suspended matter was mostly separated into a heavy and a light fraction. Separation was carried out by means of a method devised by N. PIJL, analyst at the Zoological Station (fig. 4, table 2). The sample to be analysed was transferred from the sample bottle into a strong separation funnel of one litre. A slowly rotating stirrer, performing about one revolution a second, prevented attachment of suspended matter to the glass, and kept the light material in suspension. The heavy fraction settled down and was removed from the bottom of the funnel together with a small volume of water by opening the tap for a moment. The light fraction was removed afterwards with the remaining water.

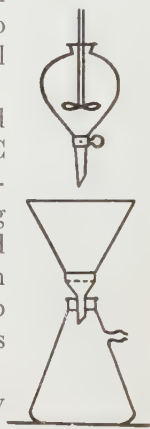


Fig. 4.
Apparatus
for separation of
suspended
matter into
a light and
a heavy
fraction

This stirring at the rate of about one revolution a second resulted in a division at a grain size of 40-60 microns. This may seem to be a somewhat arbitrary size limit, since in soil analyses clay is customarily defined as the fraction below 16 microns. Separation of the material

TABLE 2
Accuracy of the determination of sand and silt.
Duplicate samples from the harbour of Den Helder.

nr. Sample	Sand, mg/l			Silt, mg/l		
	I	II	difference	I	II	difference
1	6.1	6.5	0.4	41.1	40.3	0.8
2	5.8	6.1	0.3	39.1	38.2	0.9
3	4.1	4.7	0.6	38.9	40.6	1.7
4	3.4	4.5	1.1	23.3	21.8	1.5
5	2.3	2.8	0.5	22.3	20.1	2.2
6	6.6	7.4	0.8	39.0	39.9	0.9
7	5.8	5.8	0.0	40.2	38.1	2.1
8	9.7	10.8	1.1	51.3	51.3	0.0
9	8.9	9.9	1.0	49.7	51.7	2.0
10	7.2	7.4	0.2	51.5	50.2	1.3
11	7.3	8.8	1.5	39.3	38.5	0.8
12	5.3	5.7	0.4	35.0	34.8	0.2
13	3.1	3.1	0.0	20.1	21.8	1.7
14	3.8	4.1	0.3	22.9	20.0	2.9
mean:			0.6			1.4

at this grain size would therefore have given more generally comparable results. In the Wadden Sea, however, most clay and other particles combine to form floccules larger than 16 microns. Our interest was in the first place directed towards problems of transport of suspended matter and not to its chemical and mineralogical composition. It was therefore necessary to separate the material into two fractions without breaking down these floccules. All material behaving like sand grains larger than 40-60 microns, hereafter to be called *sand*, actually proved to consist mainly of sand. Below 40-60 microns sand played only a secondary rôle and most of the material consisted of clay, iron oxide, remains of peat and shells, and organic matter. This fraction will be called *silt*.

When checked under the microscope, the separation actually effected in the apparatus proved to be sufficiently complete. Some sand grains larger than 40-60 microns were often found in the silt fraction, but in negligible quantities.

The separation of the material into sand and silt had to take place within 48 hours after sampling. Further delay was undesirable because of the decomposition of organic matter and the tendency of silt par-

ticles to become stuck together or adhere to the glass of the bottle.

b. *Chemical composition of the inorganic part.* Attention to the chemical composition of the material in suspension is in this paper given only in so far as organic matter is concerned. The composition of the latter is dealt with in chapter IV. A chemical analysis of suspended organic matter, however, is only possible if also the composition of the inorganic part is quantitatively known, since the inorganic components, for example carbon dioxide, may influence the results.

Determinations by SCHEELE provide some information in this respect. They only refer to material collected in the harbour of Den Helder. Analyses of suspended matter from other parts of the Wadden Sea now in progress provide evidence, however, that these determinations are roughly representative of the Wadden Sea as a whole. SCHEELE's data, which have been published by VERWEY (1951), are summarized in table 3.

TABLE 3

Chemical composition of the inorganic part of suspended matter after ignition according to determinations obtained by SCHEELE in the harbour of Den Helder; VERWEY, 1952, p. 186.

Depth	SiO ₂	CaO	MgO	Al ₂ O ₃	Fe ₂ O ₃	Total
0.5 m above bottom (June 2, 3, 7, 8 and 9, 1938)	62.98	10.21	0.42	6.80	19.66	100.07
1 m below surface (June 21, 22, 23, 24, 27, 1938)	42.69	6.83	1.41	6.53	38.48	95.94
1 m above bottom (October 21, 1938)	75.6	12.8	trace	2.82	7.65	98.87
1 m below surface (October 21, 1938)	68.8	21.8	0.2	4.21	2.93	97.76

The main components are: silicate (sand and clay), iron oxide, shell sand (chiefly CaCO₃, some MgCO₃), and organic matter. Of these components clay and iron oxide may interfere with certain determinations of organic matter by loss of combined water at high temperatures; shell sand may lose carbon dioxide.

c. *Suspended organic matter.* Two different methods were followed to determine the quantity of organic material in suspension. This was necessary since both methods have their disadvantages and in this way one method could be checked with the other.

A very simple, but rather inaccurate way to determine the quantity of organic matter is by *loss of weight on ignition*. The inaccuracy is caused by simultaneous loss of carbon dioxide and water. Carbon dioxide can be determined by quantitative carbonate analyses, or removed by an acid before ignition. The first method was preferred, since the acid may also react with part of the organic matter. Filtration with 0.05 n

hydrochloric acid proved to give sufficiently accurate results. Checks were carried out on some pieces of shell to make sure that ignition over a Bunsen burner removes carbon dioxide completely. – Unfortunately, loss of combined water during ignition cannot be ascertained easily, but this loss probably did not influence the results to any considerable extent (see below).

The most accurate method for the determination of organic matter is by *elementary analysis*. This procedure moreover provides information on the chemical composition of the organic matter, as it gives the proportions of some of the principal elements present. Analyses were made for carbon, nitrogen and phosphorus. However, the method is too elaborate to be used for many hundreds of samples and could therefore be applied only to a few of them. Carbon was determined according to TER MEULEN and HESLINGA (1927), nitrogen by a micro-Kjeldahl method (catalyst $\text{HgO} + \text{K}_2\text{SO}_4$; REITH and WANSINK, 1947; BOUMAN, 1949). The method of phosphorus determination will be discussed separately hereafter (part C).

A number of determinations are collected in table 4. Comparison of the vertical columns, indicating respectively organic matter determined by loss through ignition and by carbon analyses, shows that both methods give about the same results. It may therefore be concluded, that determination of organic matter by ascertaining the loss through ignition, and subtracting the loss of CO_2 , produces more or less reliable values.

The data on nitrogen and phosphorus and the relation between C, N and P will be discussed on p. 476.

C. Phosphorus

For phosphate determinations the well-known colorimetric method of DENIGÈS-ATKINS (compare HARVEY, 1948) was followed. In some cases a modification developed by BUCH and URSIN (1948), especially suitable for brackish water, was used. According to this method all necessary reagents, with the exception of the reducing reagent stannochloride, are added to 100 ml of the sample. Before addition of the latter the phosphorus molybdate complex is transferred into 20 ml ethyl acetate by shaking twice in a separator. Reduction of the compound and development of the blue colour takes place in the acetate solution. The method is of special advantage in polluted sea water, since most pollutants are insoluble in ethylacetate. An undisturbed development of the blue colour is obtained even in fresh or brackish water coloured yellow by humic compounds. A second advantage of the method is that the phosphate of a 100 ml sample is concentrated to 20 cc, and the blue colour is more intensive accordingly. Another ad-

TABLE 4
Chemical composition of suspended organic matter. Surface samples of 10 l.

Nr sample	Date	Nr. Station ¹	Suspended matter, mg/l	A Carbonate (CO ₃), mg/l	B Loss on ignition, mg/l	B-A Organic matter, mg/l	Organic matter, calculated, mg/l	Carbon, mg/l	Nitrogen, mg/l	Phosphorus, mg/l	C:N:P
1	15-11-1950	17	30.7	2.2	7.4	5.2	4.7	2.0	—	0.061	33 : — : 1
2	15-11-1950	9	30.9 43.6	2.5 3.4	7.6 8.8	5.1 5.1	4.1 5.0	1.8 2.2	0.37 0.39	0.035 0.051	51 : 10.6 : 1 43 : 7.7 : 1
3	15-11-1950	1	— 60.5	— 4.2	— 8.6	— 4.4	— 4.6	2.1 2.0	0.42 —	0.072 0.036	29 : 5.8 : 1 55 ⁵ : — : 1
4	18-11-1950	Den Helder Harbour	55.3	3.8	10.1	6.3	6.0	2.6	0.41	0.072	36 : 5.7 : 1
5	20-1-1951	1	23.8 27.7	1.8 2.1	5.7 6.3	3.9 4.2	3.7 3.2	1.6 1.4	0.31 0.26	— 0.032	— 44 : 8.1 : 1
6	20-1-1951	S. Texelstroom	29.0 24.7	2.3 2.6	4.6 5.7	2.3 3.1	2.1 3.0	0.91 1.3	0.13 0.32	0.023 0.048	39 ⁵ : 5.7 : 1 27 : 6.7 : 1
7	13-2-1951	1	16.3 12.8	1.6 1.3	4.2 3.4	2.6 2.1	2.8 2.4	1.2 1.05	— 0.21	— 0.019	— 55 : 11.0 : 1
8	13-2-1951	17	18.0 12.8	2.1 1.1	5.2 3.1	3.1 2.0	2.3 2.2	1.0 0.96	0.17 0.18	0.026 0.021	38 ⁵ : 6.5 : 1 46 : 8.6 : 1
			36.5 45.7	3.0 2.8	5.8 5.9	2.8 3.1	2.0 2.8	0.87 1.2	— 0.19	0.023 ⁵ 0.041	37 : — : 1 29 : 4.6 : 1
Average											40 : 7.4 : 1

¹ The numbers refer to the stations of fig. 13.

² Calculated from carbon by multiplying with the factor 2.3.

vantage is that a small size colorimeter can be used for the determinations, whereas the original method requires exceptionally long colorimeter tubes.

Organic phosphorus was determined on the lines laid down by HARVEY (1948) by autoclaving the samples for six hours with sulfuric acid. HARVEY's original procedure was modified in some respects. Samples of 25 ml instead of 67 ml were used. This small volume was sufficiently large for an accurate determination since the phosphorus concentration of the area investigated appeared to be considerably higher than in the English Channel, where HARVEY collected his samples. The same quantity of sulfuric acid was added as prescribed by HARVEY (1 ml conc. H_2SO_4 , 1:1). The higher concentration of sulfuric acid in the sample can only have accelerated the decomposition of organic phosphorus to phosphate; it was found that the end point of decomposition was attained within three hours.

The samples were analysed with and without the removal of suspended matter by filtration. The difference in phosphate content between the two analyses gives the phosphorus content of the particulate material. The reliability of the method was tested by filtering some samples through filters covered with a precipitate of barium-sulphate. The suspended matter retained by the precipitate was analysed separately, and the quantity of phosphate found was compared with the difference in phosphorus between the unfiltered sample and the filtered one (table 5). Both analyses gave about the same results and the methods followed are therefore considered to be reliable.

TABLE 5

Accuracy of the determination of total phosphorus. Duplicate analyses (I and II) of samples from the Marsdiep; chlorinity ± 17.5 ‰.

Nr. sample	A. Total P, $\mu\text{g-at/l}$			B. Dissolved P, ¹ $\mu\text{g-at/l}$			A-B ²		Particulate P, ³ $\mu\text{g-at/l}$	
	I	II	Difference	I	II	Difference	I	II	I	II
1	3.16	2.98	0.18	0.85	0.78	0.07	2.31	2.20	2.16	2.41
2	2.11	2.03	0.08	0.96	1.02	0.06	1.15	1.01	1.18	1.26
3	2.14	1.96	0.18	0.96	1.08	0.12	1.18	0.88	1.13	1.21
4	1.87	1.83	0.04	1.13	1.00	0.13	0.74	0.83	0.78	0.62
5	1.82	1.71	0.11	1.02	0.86	0.16	0.80	0.85	0.81	0.75
6	1.82	1.70	0.12	0.93	0.81	0.12	0.89	0.89	0.84	0.71
7	1.76	1.70	0.06	0.83	1.01	0.18	0.93	0.69	0.95	0.87
8	1.73	1.62	0.19	0.98	1.13	0.15	0.75	0.39	0.60	0.76

¹ Including phosphate. ² Particulate P, determined by subtracting B from A.

³ Particulate P, directly determined from suspended matter after destruction with conc. H_2SO_4 .

As will be discussed in chapter IV of this paper, the phosphorus content of the particulate material is considered to be a rough measure for the quantity of organic matter present, the phosphorus percentage

of organic matter being more or less constant. The possibility cannot be excluded, however, that part of the suspended phosphorus is present in an inorganic state, for example as iron phosphate.

HARVEY (1937, 1948) determined the dissolved phosphate content of a turbid sample of coastal North Sea water before and after removal of the particulate matter. He found respectively 0.35 and 0.12 $\mu\text{g-at/l}$ of phosphate and suggested that the difference was due to particulate inorganic phosphorus dissolved by the acid reagent.

In the English Channel COOPER (1948) found a relation between "abnormal" phosphate values (values much higher than those of the other samples of the same series) and the presence of particulate iron. On theoretical grounds he assumed that iron phosphate is preferably formed in a slightly acid environment, for example in the guts of animals, and brought into the seawater in the form of faeces.

In view of these assumptions the Wadden Sea should be a favourable environment for the formation of iron phosphate. Iron hydroxide is found in large quantities in the water as well as in the bottom and there is a dense population of bottom animals, especially molluscs. According to our own determinations a water sample, containing 30–40 mg/l of suspended matter, shows a difference of 0.20–0.40 $\mu\text{g-at l}$ if treated with acid before or after filtration. If this quantity were actually present in an inorganic state, the inorganic fraction would include a considerable part of all particulate phosphorus present.

In part IV of this paper it will be shown, however, that the organic carbon-phosphorus relation of the particulate matter is comparable with the relation generally accepted for phytoplankton. Moreover, in the same section evidence of a distinct seasonal variation of particulate phosphorus, which runs parallel with the cycle of organic matter, will be supplied. Both observations do not point to an important rôle of suspended inorganic phosphorus. It would seem that HARVEY's suggestion, that all phosphate released from suspended matter by a short treatment with acid is of inorganic origin, is open to question. Perhaps part or even most of the phosphate is the product of easily hydrolysed organic phosphorus. This point deserves further investigation.

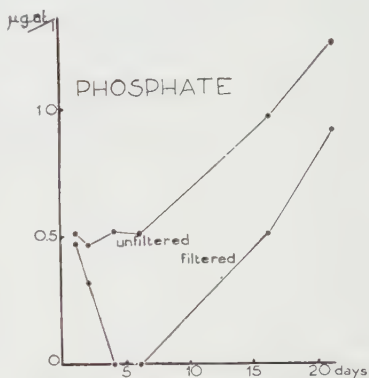


Fig. 5. Phosphate changes occurring in a water sample stored in the dark; one part has been stored with suspended matter, the other without. The unfiltered part contained about 50 mg/l of particulate material, including about 8 mg of organic matter.

Phosphate and phosphorus determinations were as a rule made immediately after sampling. Therefore, no measures against decomposition of organic material were taken. The rate of decomposition in summer (temperature 17°C) appears from fig. 5. The samples were kept in closed bottles in the dark. It is interesting to note the difference between the filtered sample and the unfiltered one. In the first bottle the phosphate content rapidly decreased to zero, after which an increase took place. According to RENN (1937) this phenomenon can be explained by assuming intensive absorption of phosphate by bacteria during the first few days of storage. After this period the number of bacteria decreases and part of the phosphate is regenerated. – In the second case it must be assumed that mineralisation of phosphorus from suspended organic matter prevented the decrease of the phosphate concentration.

D. Chlorophyll

Part of the suspended matter consists of living or dead phytoplankton or other plant material, containing chlorophyll. For the determination of the latter a method developed by KREY (1939) was used. A ten litre sample proved to be more than sufficient for an accurate determination, also in winter when the chlorophyll concentration is low. The suspended matter collected on a filter disc of normal hardness was dried and weighed, and chlorophyll was extracted by means of methyl alcohol (15–45 ml). The extraction mostly took place overnight.

The chlorophyll content of the extract was determined by means of a spectrophotometer at a wave length of 6660 \AA and a spectral width of 200 \AA . For standardization chromatographically pure chlorophyll *a* (Sandoz, Basel) was used. The pure chlorophyll was kindly supplied by Dr. J. B. THOMAS of the Biophysical Research Group at Utrecht.

II. HYDROGRAPHY; THE EXCHANGE OF WATER BETWEEN WADDEN SEA AND NORTH SEA

The main purpose of this chapter is to arrive at an estimate of the water exchange between Wadden Sea and North Sea. The calculations will be based on salinity figures and the quantities of fresh water supplied by the IJsselmeer. For the study of salinity the papers published by VERWEY and the author in 1950 could serve as a starting-point. It is proposed to follow up a summary of these papers by new observations.

Although not in open communication with a river the Wadden Sea can be considered an estuary. Therefore, the general principles of water movement in estuaries will be discussed first. Next, these principles will be applied to the Wadden Sea itself. The knowledge of water

movement obtained in this way will be used to study the transport of IJsselmeer water through the area under consideration to the North Sea. It will be shown how the rate of water exchange can be computed from this transport. The system of calculation followed is generally applicable to well mixed estuaries.

I. DISTRIBUTION OF SALINITY AND TEMPERATURE

In the Wadden Sea tidal currents continuously transport large volumes of water. This transport in itself is enough to cause considerable changes in the distribution of salinity or other variables from moment to mo-

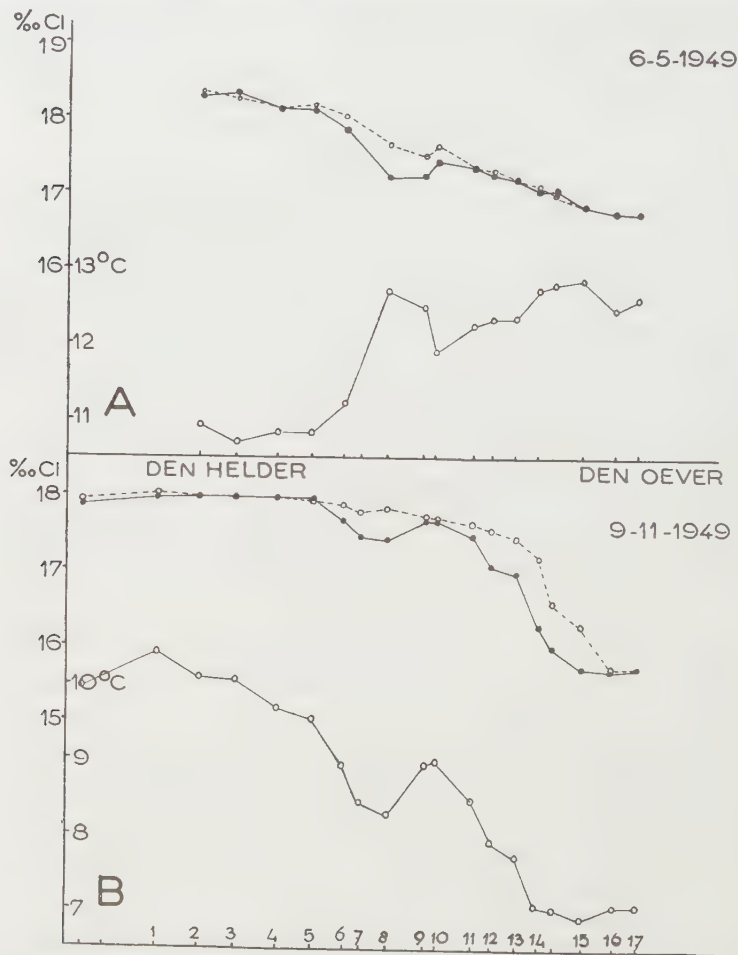


Fig. 6. Salinity and temperature along the section indicated in fig. 13; A: observations in spring; B: observations in fall.

ment. Water temperatures, moreover, vary as a result of warming and cooling, and salinity varies in consequence of variations in the supply of fresh water.

Changes in air temperature are followed by the water more closely in shallow than in deep areas.

Therefore, in periods of rising temperature (Febr.-August) the water temperature increases in proportion as one moves from the tidal inlet to the coast (fig. 6 A), whereas the reverse is the case during the time of falling temperature (fig. 6 B).

The discharge of fresh water through the IJsselmeer sluices causes a considerable decrease in salinity from the North Sea inwards (fig. 6 A and B). The salinity gradient varies along with the quantity of fresh water discharged and is greatest in winter during periods of abundant supply. In summer there are frequent periods in which no differences in salinity occur.

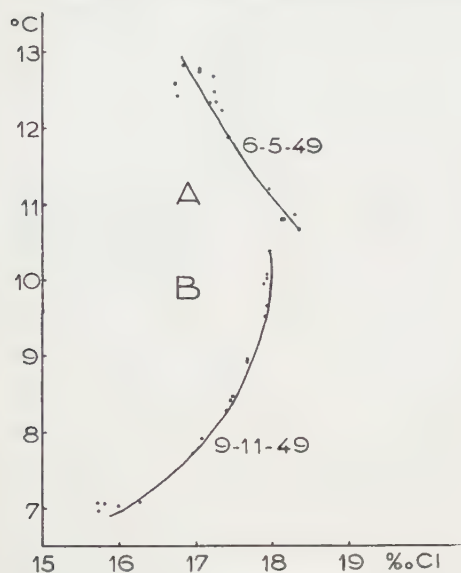


Fig. 7. T-S-relation of the observations of fig. 6.

If simultaneous observations in one particular Wadden Sea channel are considered, a close correlation between temperature and salinity becomes apparent (fig. 7). In summer the water temperature increases along with a decrease in salinity; the reverse happens in winter. The relation holds for both bottom and surface samples (fig. 8), but is different for different channels (POSTMA and VERWEY, 1950). This means that mixing within one channel area is intensive, but that the water masses of adjoining channels are as a rule well separated from one another by the intervening flats.

If we compare the readings obtained at any particular point, we find that the tidal movements cause periodical changes in temperature and salinity. The geographical distribution of these variables can therefore only be found by simultaneous observations, for example at high tide, in many places. Fig. 9 shows the distribution of salinity at high water in the first few days of August, 1948. The isohalines for different dates may show large variations and the same applies to the isotherms of different dates, but the general pattern is always more or less the same (POSTMA, 1950).

The changes in temperature and salinity distribution in the course of the tide are rather complicated and difficult to describe in detail. A short and schematic description of some of the principles probably

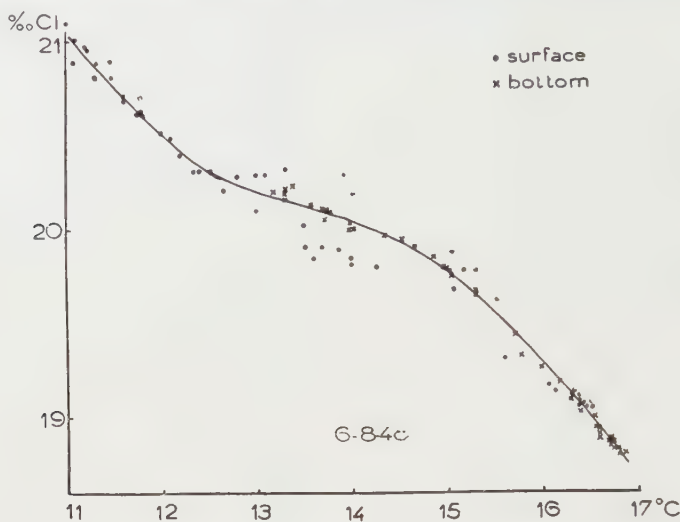


Fig. 8. T-S-relation of the observations of fig. 11.

involved may suffice here, since the subject is discussed more extensively in the papers mentioned before.

To simplify matters we may represent the Wadden Sea as consisting

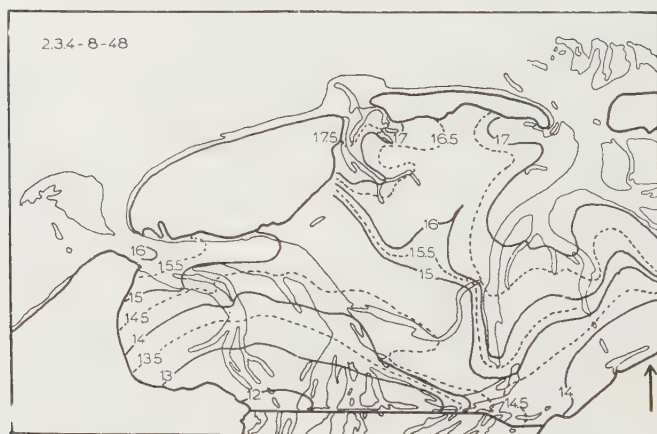


Fig. 9. Chlorinity distribution at high tide in the early part of August 1948; fresh water had been discharged at Den Oever and Roptazijl (marked by an arrow), but not at Kornwerderzand.

of one tidal inlet and one channel with shallows on both sides. The shallows are taken to emerge at low tide (fig. 10 a). The flood tide is supposed to enter the area from the North Sea and the rising water to spread over the flats. A few isohalines chosen at random will serve to illustrate the point.

Observations such as those given in fig. 9 show that the isohalines move farther inward along the channel than on the flats (fig. 10 b). To explain this it must be realized that the influence of bottom friction on water movement is relatively more considerable in shallow water than it is in deep. Hence currents have smaller velocities on the shallows than in the channel.

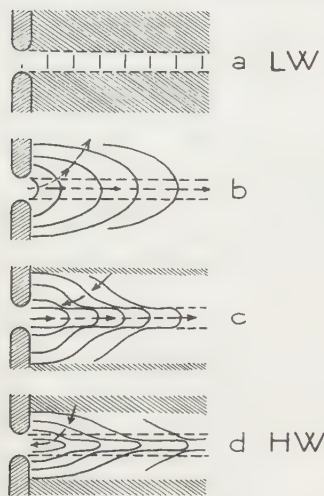


Fig. 10. Scheme of the changes of isohalines during a tidal period.

Further, in shallow water the reversal of the slope of the area surface at high tide is immediately followed by a reversal of the current, whereas in deeper water there is a considerable time lag between the two phases (compare figs. 23, 24 and 25). As a result the ebb tide starts earlier on the flats than in the channel. This must also be explained from the fact that bottom friction is more considerable on the flats than in the creeks; at the turn of the tide the energy of the flood current is used up more rapidly in shallow than in deep water.

As a result of this phenomenon the water in the channel is still running inward when the water on the shallows is already ebbing.

This causes a marked transformation in the pattern of isohalines. The strongest deflection is generally observed along the edge of tidal flats, where the bottom slope is steepest (fig. 10 c). Here a salinity gradient, which forms a sharp dividing line between the water masses on either side, is generated. Salinity – hence mostly density – is greatest on the channel side of this gradient, because the channel water comes from farther seaward than the water on the shallows.

During the later phases of the ebb the water running back from the shallows pushes the boundary between the two water masses in the direction of the channel axis (fig. 10 d). Perhaps this movement is supported by differences in density, the lighter water moving over the heavier subsurface water.

After the current in the channel has also turned, the boundary is shifted seaward and disintegrates gradually. It can be observed, however, as a streak (STOMMEL, 1951) during a large part of the

ebb tide. Flotsam and foam, unable to cross the boundary, are accumulated in these streaks or tide-rips, often forming clearly visible lines.

The disintegration of the streaks is caused by the strong ebb current. At the end of the ebb-tide mixing is often complete. If during the ebb-tide the water is not completely drained off from the tidal flats, new streaks may develop at low tide. After low tide they move, however, away from the channel and are therefore not observed so easily. Measurements have shown that the more saline water in this case occurs on the shallow side of the boundary.

If for a moment we consider the water on the shallows (at high tide) and the water in the channel to represent two separate bodies of water which do not mix, it is of importance to note that the phenomenon described must cause a mutual shifting of these two water masses. The water carried from the channel on to the flats by the flood tide appears, after its return, to have been displaced seaward in respect of the water that remained behind in the channel. In a deep channel as the Texelstroom this displacement may even amount to some 3 kilometres.

The seaward movement of the water returning from the shallows after high tide is more or less neutralized, however, after low tide, since then this water, after leaving the channel, becomes more or less stagnant, whereas the ebb current in the channel continues. This causes again a mutual shifting of the two water masses, but now in a reversed sense: the channel water is displaced seaward with respect to the water of the flats.

The ultimate effect as regards water movement is therefore practically nil. The process has, however, an important bearing on water exchange, since actually the water returning from the flats is mixed thoroughly with the channel water. Water masses, originally separated by distances of several hundreds of metres or even some kilometres, are thus mixed thoroughly. The horizontal exchange of water is strongly promoted in this way.

It also fits in with the above explanation that differences in salinity between bottom and surface are mostly greater during the ebb-tide than during the flood. The water returning from the nearby shallows has a lower salinity than the channel water, which originates from farther seaward. As a result, the vertical salinity gradient will therefore increase after high tide (fig. 11).

This increase, however, might also be explained as follows. The flood runs with the horizontal salinity gradient, the ebb against it, while in both cases the current velocity decreases from bottom to surface. Therefore, during the flood the surface water comes on top of

bottom water of lower salinity than was originally the case, causing a decrease in stratification, whereas during ebb the upper water layer comes on bottom water of greater salinity, so that stratification increases.

In the case of fig. 11 it can be shown, however, that the latter effect cannot play an important rôle in causing stratification during the ebb-

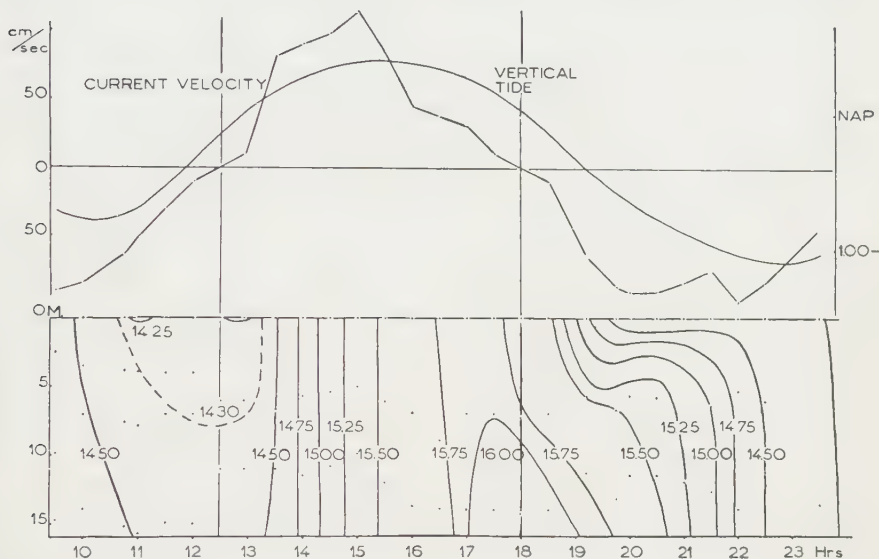


Fig. 11. Observations of vertical and horizontal tide and of salinity at station 3 of fig. 13 (30 March 1950).

tide. Two hours after the beginning of the flooding tide the salinity rises above 15^{0}_{00} Cl (14.20 h.). From this moment onwards, until slack high water, the 15^{0}_{00} isohaline was carried inward along the channel axis over a distance of about 7.4 km¹. Nevertheless, the surface salinity drops below this value nearly immediately after the beginning of the ebb movement. During this short period the surface water was carried back along the channel axis over a distance of only 0.8 km. One can therefore be sure that this decrease in salinity, and consequently also the ebb stratification, cannot have been caused by water running back through the channel, but only by the supply of less saline water from the nearby flats.

¹ The distances of 7.4 and 0.8 km have been calculated by means of the current velocity curve on the assumption that this curve is the same over the whole of the distance; actually, current velocity will decrease toward the Wadden Sea interior, so that the distances calculated will be somewhat too high.

2. THE INFLUENCE ON WATER MOVEMENT OF DIFFERENCES IN DENSITY

Hydrographically the Wadden Sea, being a transition area from river conditions to the conditions of the open sea, may be defined as an estuary. The water movement within estuaries has been studied among others by ALEXANDER, SOUTHGATE and BASSINDALE (1935) in the inlet of the river Tees (England), by TULLY (1949) in the Alberni inlet (Canada), by KETCHUM (1951) and STOMMEL (1951) in the New York Bight and other areas, by PRITCHARD (1952) in Chesapeake Bay, and by ROCHFORD (1951) in several estuaries of the Australian coast. Water movements in estuaries are to a considerable degree influenced by the density differences caused by the supply of fresh water. The relatively light river water remains in the upper water layer. On its way seaward it becomes progressively mixed with the underlying seawater and the difference in salinity between surface and lower layers, which is at first considerable, decreases. The decrease in stratification depends on the intensity of mixing, which in its turn mostly depends on tidal movement. Sometimes wind plays an important rôle.

Salinity always increases seaward in the upper as well as in the lower water layers. The quantity of fresh water transported to the sea in unit time must on an average be the same as through every transverse section of the estuary, and also equal to the quantity flowing from the river in unit time. The total quantity of water moving seaward in the upper water layer must increase, since the admixed sea water must be taken along. The seaward movement of salt water in the upper layer is compensated by transport of salt water within the lower layers in an opposite direction (fig. 12). The transport of fresh water to the sea in the upper layer therefore causes a seawater circulation from the open sea into the area along the bottom and from the area back to the open sea along the surface. The energy for the transport of the river water itself is provided by the field of density. Energy is also required for the seawater circulation, described above, since bottom water of high density must be transferred to the surface layer of lower density. This energy is provided by the forces bringing about vertical mixing, viz. the tides, sometimes the wind.

It will be clear that in the system described, transport of fresh water quickens the rate of water exchange between estuary and sea and

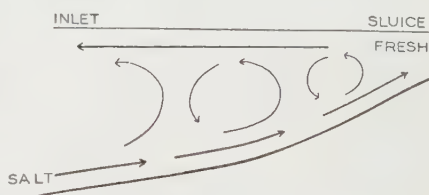


Fig. 12. Scheme of water circulation in a well stratified estuary.

renewal of the subsurface layers. Nevertheless, part of the bottom water can be stagnant, especially if there is a bottom elevation in the inlet, as is often the case.

In order to study the question of the transport of fresh water through the Wadden Sea, a representative section was chosen, running from one of the IJsselmeer sluices through a tidal channel to the North Sea. Here, salinity measurements were carried out regularly, especially around high tide (fig. 13). The marked variations in salinity called for a long series of observations. These were continued at intervals of about one month for three years (1949, 1950 and 1951). From these

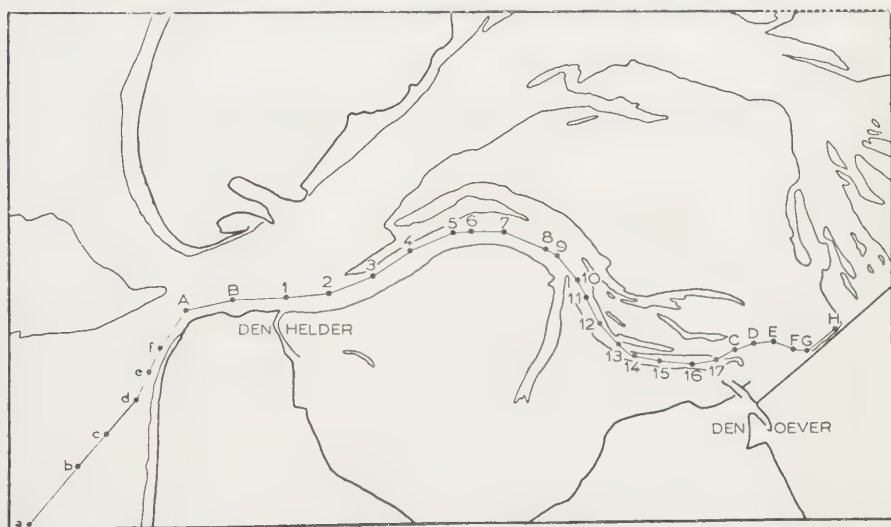


Fig. 13. Main section of investigation; location of the stations, where measurements were carried out monthly during 1949, 1950 and 1951.

data the average curve of salinity given in fig. 14 A was derived. In order to obtain the average horizontal distribution of salinity of the area investigated, this curve has been combined with data from salinity surveys such as the one of fig. 9 (fig. 14 B). The distribution of fig. 14 B applies to cases when fresh water is only discharged at Den Oever. The original data used for the construction of figs. 14 A and B are not given here in detail, but are on file at the Zoological Station.

Usually large quantities of water are also discharged at Kornwerderzand (table 1). Probably about one half of the supply from this sluice (3.3×10^6 m³/ tide) moves seaward through the area investigated, the other half leaving the area through the Vlie area (POSTMA, 1950). Therefore, about 25% of all fresh water present in the area studied originates from Kornwerderzand and 25% from Den Oever. However, along the section from Den Helder to Den Oever the influence of Kornwerderzand will be much smaller, probably less than 5%. Another interfering factor is the

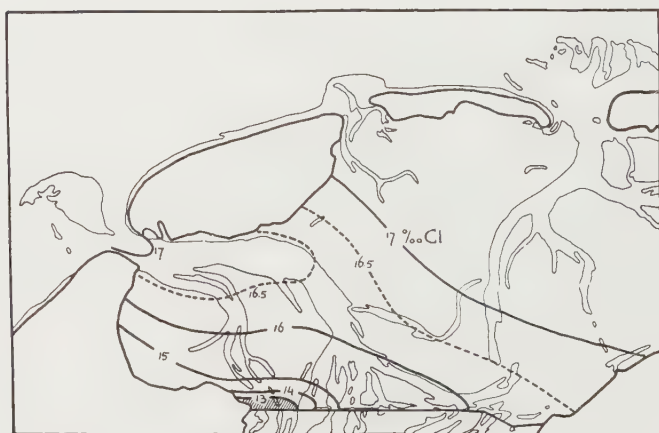
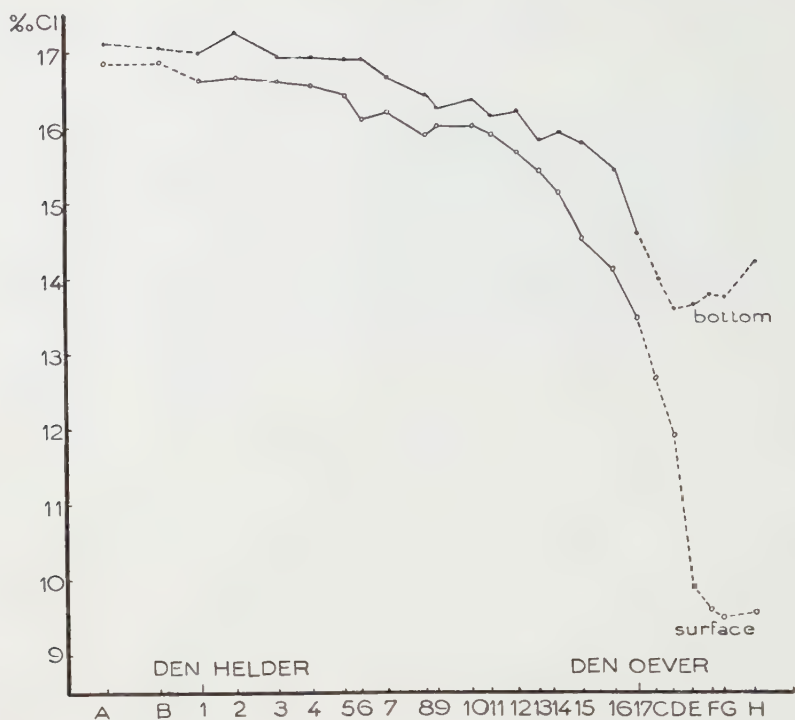


Fig. 14. A: average distribution of salinity along the section of fig. 13. B: average horizontal distribution of salinity of the area investigated, when fresh water is only discharged at Den Oever.

supply of fresh water at Den Helder (table 1) and south of this town. All things considered, about 10% of the fresh water along the section studied may not have originated from Den Oever. As the calculations to be carried out are comparatively rough, this percentage will be left out of account.

In comparison with horizontal differences, the vertical differences in salinity are generally low (about 0.5 ‰ Cl). A more pronounced stratification only exists near the IJsselmeer sluice. If we leave this area out of account for a moment, we find that transport of fresh water can only take place through the seaward movement of enormous quantities of water at the surface and the opposite movement of similar quantities along the bottom. This may be elucidated by the following calculation.

The average chlorinity of the western part of the section Den Helder-Den Oever amounts for the bottom layer to about 16.5, and for the surface layer to 16 ‰; the chlorinity of the North Sea water entering the Wadden sea amounts to 17 ‰ Cl. From these figures it can be calculated (in the way to be described on p. 432) that every m³

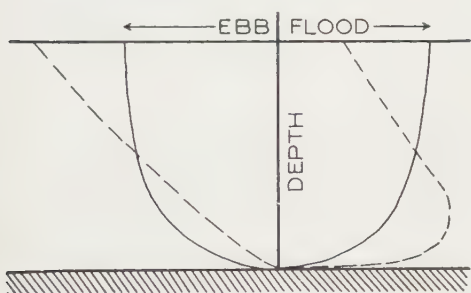


Fig. 15. Vertical distribution of current velocity during ebb and flood. For explanation see text.

of the surface layer contains only $1/17$ m³ of fresh water and the bottom layer only $1/34$ m³. For the transport of 1 m³ of fresh IJsselmeer water it would therefore be necessary to move about 34 m³ of surface water seaward and about the same amount of bottom water in the opposite direction. Actually, an average of 10×10^6 m³ of fresh water is discharged at Den Oever during every low tide (table 1).

This transport would therefore involve an estuarine circulation of 0.34×10^9 m³ of Wadden Sea water of 16–16.5 ‰ Cl.

If, however, such an estuarine circulation were to go on in addition to the ordinary movement of water caused by the tides, this would, as is diagrammatically shown in fig. 15, lead to great differences between the strength of ebb and flood currents at the bottom and at the surface. The full-drawn curves in fig. 15 (after VAN VEEN, 1937) schematically represent the average vertical distribution of current velocity in the absence of salinity (density) differences (with ebb and flood curves about symmetrical), while the dotted lines show the approximate deflections that would be caused by the estuarine circulation (with ebb and flood curves quite asymmetrical). The estuarine circulation would increase the ebb current at the surface and the flood current near the bottom,

whereas the flood current at the surface and the ebb current near the bottom would show a decrease. In our case the velocity of the surface currents would be about three times greater during the ebb-tide than during the flood.

Such a difference between the velocities of ebb and flood currents, though far greater than the possible error of observation, has never actually been measured. All measurements, on the contrary, indicate that ebb and flood currents are of about the same strength, for which fig. 11 may serve as an example. The average flood current at the surface in this instance amounts to about 60 cm/sec., the average ebb current to 70. Although the former is indeed somewhat smaller than the latter, the difference between the two is small, and other measurements, particulars of which need not be given here, show the same results or even a smaller difference. This means that this combination of estuarine and tidal circulation fails to give an adequate explanation of the transport of fresh water seaward. It must be assumed that the strong tidal circulation causes such an intense mixing that the fresh water is divided more or less equally over both surface and bottom water, so that no estuarine circulation is developed. It will at best play a rôle in the vicinity of the IJsselmeer sluices, where fresh stratification of water masses goes on all the time.

Generally speaking, the fresh water is therefore not transported as a surface layer, but as part of a mixture which is of about the same composition near surface and bottom. Exchange of water between Wadden Sea and North Sea will take place at about the same rate for both fresh and salt water. Since differences in density may be assumed not to play an important rôle in water movement, the only remaining forces that can bring about an exchange are tidal movement and wind, which cause horizontal and vertical mixing of water masses. The mutual shifting of water masses of channels and tidal flats, described on p. 424, may have a special bearing in this respect.

The fact that the influence of fresh water on water movement in the Wadden Sea is of secondary importance becomes especially clear, if we compare tidal forces with the forces caused by the field of density.

The force exerted by the tide is proportional to the slope of the water surface. The degree and direction of the slope change in the course of the tide. On an average however, the slope along the special section studied (compare fig. 13), derived from tidal gauge observations at Den Helder and Den Oever, is about 3 cm per km (measured along the tidal channel), directed inward during the flood and seaward during the ebb. The field of density can be derived from the distribution of salinity and temperature. The average horizontal distribution of salinity at high tide, already given in fig. 14, has been combined with details of the vertical distribution obtained from observations like those of fig. 11. The temperature is considered to be the same all over the section and equal to the yearly average of 11°C. In that case the lines of equal density coincide with the isohalines (fig. 16).

From the field of density the slope of isobaric surfaces can be determined, if the position of zero level can be indicated. This position is approximately estimated on the following grounds. Above level surface isobaric surfaces slope in the direction of the sea and forces are exerted in that direction. Below zero level the reverse is the case and forces are exerted in the direction of the land. The sum of all horizontal forces must be about equal, since the ultimate horizontal transport of water is practically

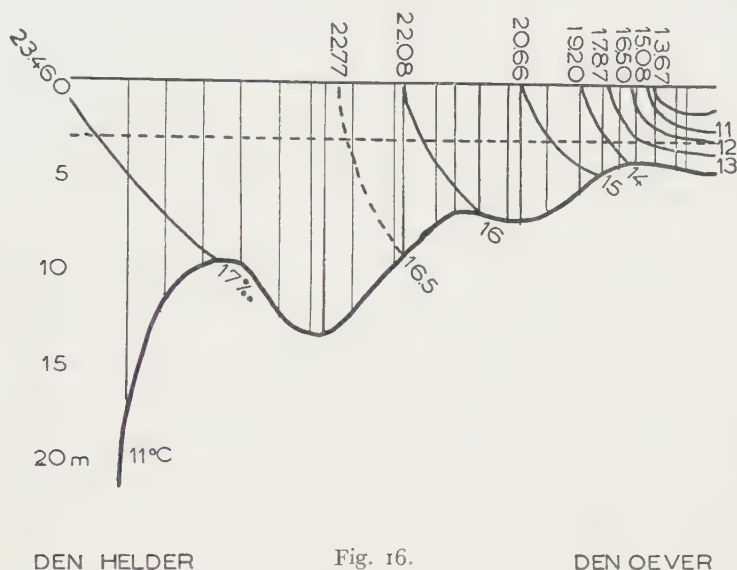


Fig. 16.

nil. The small quantity of fresh water discharged is of no importance in this respect. As bottom friction also exerts a horizontal force, it is difficult to estimate the exact position of level surface, but it must be situated somewhere between the bottom and the water surface. Assuming its position to be about 3 meters below the water surface (compare fig. 16) it can easily be computed from the field of density that the relative slope of the upper isobaric surface, which coincides with the water surface, must be about 0.2 cm per km, near the sluice about 0.5 cm/km. The slope of all other isobaric surfaces is smaller.

The forces exerted by the field of density are proportional to the slope of the isobaric surfaces. The number of 0.2 cm/km may therefore be compared with the 3 cm/km calculated for the slope caused by the tide. The conclusion can be drawn that the influence of the field of density on water movement must be smaller than the influence of the tide.

3. THE TRANSPORT OF FRESH WATER

It may be concluded from the preceding discussion that in the Wadden Sea vertical mixing prevents the development of marked stratification. This means that the velocity of transport of fresh water through the estuary to the sea mainly depends on the rate of water exchange between Wadden Sea and North Sea. Conversely, it must be possible to

calculate the water exchange from the rate of transport of fresh water. The calculation of the latter will be based on the following line of thought.

From water volumes and salinity one should be able to estimate the total amount of fresh water present in the part of the Wadden Sea through which the fresh water from the IJsselmeer is transported to the North Sea. The relation between this amount and the quantity discharged per tide would then be known. If the former amount were three times as large as the latter, this would mean that in the course of every tide one third of the fresh water present in the Wadden Sea would be carried to the North Sea. One could also say that the fresh water requires three tides for passing through the Wadden Sea; this period has been termed flushing time by KETCHUM (1951).

The main difficulty is to estimate the amount of fresh water present. The calculation will be restricted to water originating from Den Oever and therefore be based on figs. 14 A and B.

The volume of fresh water, V_f , present within a certain volume V of estuarine water, can be computed from the salinity, S_n , of the volume in question and the salinity, S , of the sea water outside the estuarine region, according to this formula:

$$V_f = \frac{S - S_n}{S} \times V \quad (1).$$

The amount of fresh water present within the Wadden Sea can therefore be calculated, if the chlorinity of the incoming North Sea water, and the salinity and water volume of the area concerned are known. The average chlorinity of 17‰, measured in the (tidal) inlet, will be held to be the chlorinity of the sea water entering the Wadden Sea. The average salinity distribution of the area is given in fig. 17 A, which is based on the following method.

The diagram represents the average chlorinity along the vertical (average for three years; see table 23) for the section Den Helder-Den Oever, obtained from figures 14 and 16. Besides the average chlorin-

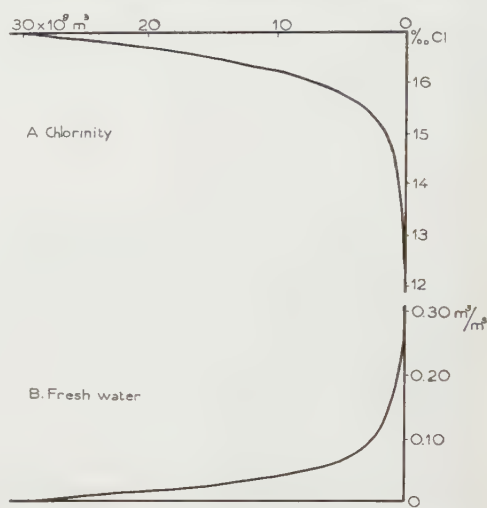


Fig. 17. Increase of salinity (A) and fall of the concentration of fresh water (B, computed from A) with increasing volumetric distance to Den Oever; for explanation see text.

ities, however, we should also know the corresponding water volumes. The horizontal axis of fig. 17 therefore does not represent the geographical distances between the stations of observation, as is the case in the above figures, but gives their volumetric distances. The latter have been obtained as follows.

Viewed from the sluice of Den Oever every isohaline of fig. 14 B compasses at high tide a certain volume of water, which volume increases with each isohaline. The enclosed volumes can be determined by means of the bottom topography of the area, which is known from observations by the Dutch Hydrographic Office. It is convenient to use these volumetric instead of the geographical distances, since thus the influence of the geographical character of the estuary is to some extent eliminated.

The distribution of fresh water within the area can now be estimated from the salinity distribution of fig. 17A according to formula (1); the result is given in fig. 17 B. As stated, the horizontal axis of this diagram gives the volumetric distance to the sluice, which has been expressed in m^3 . The vertical axis of fig. 17 B gives the fresh water content, expressed in m^3 per m^3 of seawater. Hence, every square of the diagram represents a certain volume of fresh water. The area enclosed by the fresh water line and the two axes represents the average total quantity of fresh water, which is $132 \times 10^6 \text{m}^3$.

Since the average quantity of fresh water discharged during one tide amounts to $10.3 \times 10^6 \text{m}^3$ (table 1), the total quantity present in the estuary is 12.8 times this figure. Because the average fresh water content of the Wadden Sea remains the same, the quantity flowing out into the North Sea is also $10.3 \times 10^6 \text{m}^3$ per tide or 8% of the total quantity of fresh water present in the Wadden Sea.

It is self-evident that every dissolved substance that has the same geographical distribution and gradient as the fresh water will be carried along at the same rate as the latter. This will mostly be the case with dissolved substances distributed homogeneously in the IJsselmeer water itself, but it may accidentally also hold for substances not originating from this source. Examples of this kind will be given in the following chapters. The rate of transport of such a compound can easily be determined by estimating the total quantity of the material present in the Wadden Sea and taking 8% of this figure. If a small percentage of the substance is also present in the North Sea, its concentration in the latter must first be subtracted from the values found in the Wadden Sea. It goes without saying that there is no point in such estimations, if the rate of transport can be determined directly from the quantity of the compound supplied to the area in unit time.

An improvement on the above procedure can be obtained, if we

regard the transport of fresh water to the North Sea as being caused by a process similar to diffusion. The "coefficient of diffusion" C at a particular place will then be defined by

$$R = C \frac{dV_f}{dx} \dots \dots \dots (2),$$

where R indicates the quantity of fresh water transported per unit of time, V_f the concentration of fresh water, and x the volumetric distance from the place in question to the IJsselmeer sluices. The term $\frac{dV_f}{dx}$ is represented by the degree of slope of the fresh water curve of fig. 17 B. Its value decreases according as the distance from the sluice increases. R , which represents the quantity of fresh water discharged in unit time, e.g. the tidal period, has the same value along the whole line. Therefore, the coefficient of diffusion increases according as the distance from the sluice increases, whereas in an ordinary process of diffusion this coefficient is considered to be constant.

After C has been determined, the equation (2) could be used to calculate the rate of transport of a foreign substance which has the same geographical distribution as the fresh water (isographs of the substance running parallel to the isohalines), but which has a different gradient. This might for example be the case with an unstable compound discharged with the fresh water from the IJsselmeer, and disintegrating gradually during its transport through the Wadden Sea. In the equation (2), V_f should then be replaced by the concentration of the substance actually observed. C being known, the rate of transport, represented by R , could be estimated and would in our example turn out to decrease according as the distance from the sluice increases.

The problem would become more complicated if the substance considered were to show a geographical distribution different from the distribution of the fresh water. This will in general be the case with substances not discharged into the Wadden Sea with the fresh water itself, but brought into the area at another point. If no direct measurement of the discharged quantities were possible, the order of magnitude of the transport could nevertheless be roughly estimated from the distribution of the substance in the Wadden Sea, if we take the coefficients of diffusion to be about the same as those calculated from the fresh water distribution.

4. SEGMENTATION AS AN EMPIRICAL APPROACH TO THE PROBLEM OF WATER EXCHANGE

The conclusions arrived at in the previous section would become more valuable if it were possible to develop a method which would allow us to confirm the results obtained along another way.

An attempt will therefore be made to estimate the relation between the distribution of salinity observed at a certain moment, and the quantities of IJsselmeer water discharged in a particular period preceding that moment. This relation can only be estimated if the fate of every single volume discharged is known. The total volume of fresh water present in the Wadden Sea at a certain moment is the sum of fractions of all volumes discharged within a certain period preceding the moment in question, the fractions being smaller as the discharge from which they originate is farther back in time. At first, the whole of a volume will contribute to the fall in salinity; after a few tides, however, its influence will gradually decrease, since part of it has gone to the North Sea; after a number of tides it will practically have disappeared into the latter.

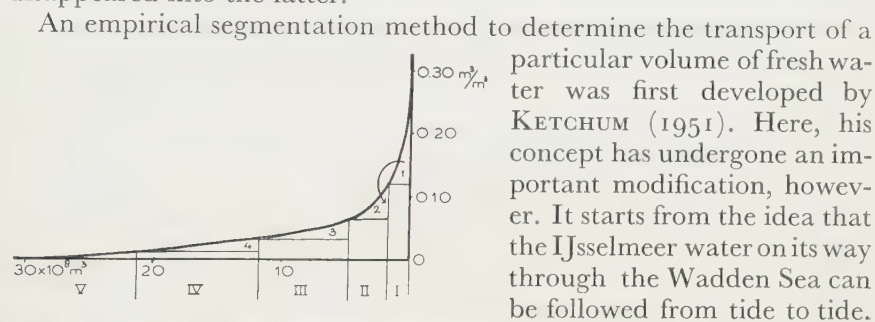


Fig. 18. Division of the Marsdiep area into segments; for explanation see text.

It is assumed that the quantity of fresh water discharged in the course of one tide will within the next tidal period reach the part of the Wadden Sea immediately adjoining the sluice, which will here be called the first segment. During the next tide the water of the first segment – which by then is supposed to have completely mixed with the fresh water – is assumed to mix completely with that of a second, and during the third tide the contents of the second are supposed to mix completely with those of a third segment, and so on.

The volumes of the segments may conceivably be determined in the following way. We have seen that the distribution of fresh water within the area studied can be represented by the diagram of fig. 17 B. The area enclosed between the lower horizontal axis, the vertical and the fresh water curve itself represents the total volume of fresh water present. The amount of fresh water displaced from segment I to segment II by complete mixing of the two segments is represented by triangle 1 (fig. 18). The volume of segment I is chosen in such a way that triangle 1 is just able to take up the amount of fresh water discharged per tide ($10.3 \times 10^6 \text{ m}^3$, see table 1). The volume of the first segment can be read off from the horizontal axis, while the total

amount of fresh water within this segment is represented by the triangle plus the rectangle below it.

The dimensions of the second and following segments are determined in the same way as the size of the first, all triangles being as large as nr. 1. If during the second tide segments II and III become completely mixed, this will cause a displacement of an amount of fresh water of the size of triangle 2 from the inner to the outer segment. If this process is applied to every pair of segments the result will be a shifting of all triangles over the distance of one segment. As all triangles have the same area, the amount of fresh water in every segment will remain unchanged, the first segment receiving fresh water from the IJsselmeer, the last segment supplying fresh water to the North Sea.

The dimensions of the segments depend on the slope of the fresh water line: the steeper this slope, the smaller the range of the segment. The segments grow larger in the direction of the North Sea; this is comprehensible since current velocity increases in the same direction and therefore also intensity of mixing and water exchange. The area studied is found to contain four complete segments and part of a fifth. If segment V has about the same range as segment IV, about three quarters of the former fall within the circumference of the Wadden Sea.

The above representation of discontinuous water exchange from segment to segment is only intended to be a useful means for calculations; it is self-evident that it does not represent the actual process of exchange. The very supposition that mixing will be complete over a certain distance within a certain time, in our case one tide, cannot, of course, be true. On the other hand, water exchange is not a continuous process comparable with diffusion, as supposed earlier, but it is connected with the tidal cycle. One particular volume of fresh water can often be followed for a few tides, becoming progressively mixed with the seawater, but still clearly distinct from the environment. This characteristic is brought out better by the segmentation method. During the first high tide after its discharge the volume of fresh water will find itself within the limits of the first segment, in the next tidal period its boundaries will have reached the end of the next one, etc.

As stated, the concept of segmentation set forth above has been derived from an empirical method to investigate water exchange in estuaries, developed by KETCHUM (1950, 1951). His method of segmentation is, however, quite different from the one followed above. The limits of his segments are defined by the distance over which a particle of water moves on the flooding tide. The percentage of water, placed within a segment during one tide, is determined by the ratio in which the intertidal volume stands to the high tide volume, the intertidal volume being the volume difference of the segment between high tide and low tide. A great advantage of the method is therefore that calculations of the rate of exchange are only based on easily available

data as volume of river flow, geographical shape of the estuary and the range of the tide. Computations carried out by KETCHUM on a number of different estuaries showed that the calculated distribution of salinity agrees with the distribution actually observed.

Although KETCHUM did not express himself in this way, his method essentially implies that after low tide pure sea water enters the estuary with the flood, covering the area with a layer of undiluted sea water, which in the first instance does not mix with the estuarine water. The thickness of this layer, which is assumed to penetrate as far as the head of the estuary, would be equal to the tidal amplitude. At high tide complete mixing with the estuarine water would take place. Next, the mixture is supposed to be transported seaward by the ebb movement.

According to this method every segment is supposed to be in direct contact with the open sea. Our own method supposes that every segment exchanges water only with its neighbours. For this reason, mutual comparison of the two procedures is difficult.

The segmentation of the Wadden Sea, as determined above, will be used to estimate the transport of a particular volume of fresh water

TABLE 6

The movement through the Marsdiep area of a separate volume of fresh water sluiced at Den Oever; for explanation see text.

[illegible]

discharged at Den Oever. During the first high tide after the discharge this volume is supposed to be divided evenly over the first segment. The distribution of the volume at the following tides is determined on the supposition that mixing of neighbouring segments is completed in one tidal cycle. The distribution calculated for successive tides after the discharge is given in table 6, where the initial volume is put at 100. As can be seen in fig. 18 the Wadden Sea appears to contain between four and five segments and calculations are therefore given for both cases.

During the first tide the volume of 100 is supposed to be introduced into segment I. During the second tide complete mixing of the segments I and II will distribute this volume homogeneously over these segments. As segment II has a larger volume than I (3.2 against $1.6 \times 10^8 \text{ m}^3$), the former will then contain most of the fresh water (67 against 33). During the third tide mixing of the segments I and II causes no redistribution of the fresh water over these segments, since they have been mixed completely already during the preceding tide. Mixing of II and III, however, will introduce fresh water into III at the expense of II. During the fourth tide mixing of II and III will have no effect, but mixing of I and II will carry fresh water from I to II until the ratio $1.6:3.2$ has again been attained. During this tide mixing of III and IV will cause transport of fresh water to segment IV, etc.

Segment V is incomplete and it has therefore been assumed that its volume is equal to that of segment IV. Exchange between the last segment and the North Sea has been supposed to deprive this segment of all fresh water supplied to it during the preceding tidal cycle.

During the first four to five tides there is no loss of fresh water to the North Sea; after that period the fresh water gradually disappears. The decline is more rapid with four than with five segments, see also fig. 19, curves A and B. However, neither curve A, nor curve B indicates the

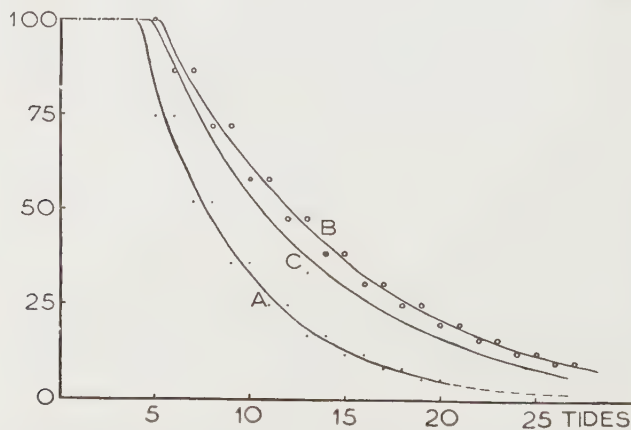


Fig. 19. The percentage present in the Wadden Sea of one particular discharge of fresh water after a number of tides.

actual decrease. The position of the intermediate curve C, which is more exact, has been approximately determined by assuming that the ratio of the difference in volume between the values indicated by A and C to that between the values of A and B is equal to the ratio of the volume of the incomplete segment V present in fig. 18 to the volume of the complete segment V.

Curve C allows us to estimate how much has remained of a particular volume of fresh water a certain number of tides after the discharge. After 23 tides about 10% of the original volume is left. If the same amount of fresh water was discharged at every tide, the quantity of

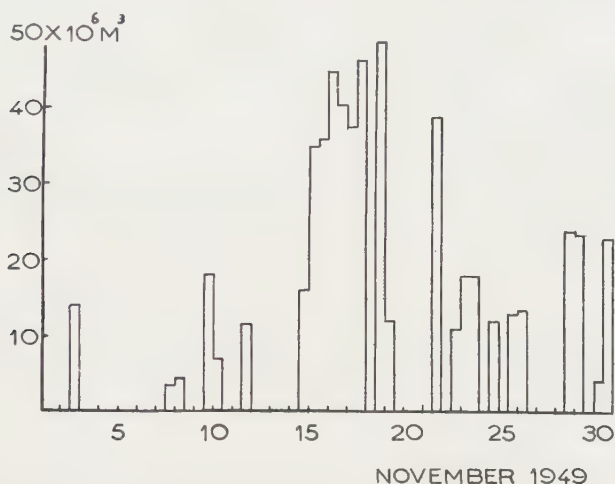


Fig. 20. Example of the discharge of fresh water at Den Oever.

fresh water remaining from tide 23 and earlier tides would amount to about 5% of all fresh water present. For the determination (from discharge data) of the total amount of fresh water present in the Wadden Sea at a given time, it is mostly considered sufficient to take into account 22 tides previous to that moment.

We shall for a moment assume that at every low tide the same amount of fresh water is discharged at Den Oever. In that case, and provided a steady state has been attained, the area below the curve C of fig. 19 represents the total quantity of fresh water present in the Wadden Sea. This area is found to be equal to about 13 discharge units. On p. 433 this quantity has been estimated to amount to 12.8 units. The agreement between the two estimates supports the empirical segmentation method followed.

After having estimated the rate of transport of one particular volume

of fresh water, we may in conclusion return to our starting-point, which was: how to determine the relation between the distribution of salinity observed at a certain moment and the quantities of fresh water discharged in a particular period preceding that moment.

As has been said before, the salinity figures have been found by monthly observations around high tide from Den Helder to Den Oever (table 23); the volumes of IJsselmeer water discharged at Den Oever are known from measurements by the "Dienst van de Zuiderzeewerken". Fig. 20 gives an example of this discharge for the month of November, 1949.

For every monthly set of salinity observations a diagram similar to that of fig. 17 A, representing the rise of salinity along with increasing volumetric distance to Den Oever, has been drawn and the corresponding volume of fresh water has been derived from it in the way described for the average distribution on p. 433. The values found are given in column 3 of table 7.

The amount of fresh water present within the Wadden Sea as the remainder of the water discharged during the 22 previous tides is given in column 4 of this table.

TABLE 7

Comparison of the accumulation of fresh water determined from the salinity surveys with the accumulation calculated from discharge data; Marsdiep area.

Nr.	Date	Calculated from salinity	Calculated from discharge	Nr.	Date	Calculated from salinity	Calculated from discharge
		$\times 10^6 \text{ m}^3$	$\times 10^6 \text{ m}^3$			$\times 10^6 \text{ m}^3$	$\times 10^6 \text{ m}^3$
—	13- 7-48	237	257	19	10- 5-50	354	332
1	26- 1-49	349	213	20	3- 6-50	217	147
2	16- 2-49	95	133	21	3- 7-50	131	131
3	24- 2-49	77	6	22	1- 8-50	234	74
4	6- 5-49	94	16	23	31- 8-50	98	163
5	14- 7-49	0	0	24	19- 9-50	20	96
6	27- 7-49	0	0	25	19-10-50	190	181
7	13- 9-49	0	0	26	15-11-50	48	158
8	20-10-49	0	0	27	18-12-50	293	351
9	22-10-49	62	76	28	10- 1-51	113	168
10	25-10-49	45	150	29	13- 2-51	133	224
11	1-11-49	359	245	30	28- 2-51	221	231
12	9-11-49	82	33	31	13- 3-51	213	173
13	12-12-49	180	219	32	17- 4-51	51	236
14	9- 1-50	237	200	33	5- 6-51	118	42
15	7- 1-50	135	69	34	13- 7-51	28	200
16	22- 2-50	205	268	35	29- 8-51	170	198
17	13- 4-50	0	0	36	5-11-51	345	272
18	24- 4-50	54	6				

The relation between the total quantities of fresh water determined from salinity and discharge figures is given in the diagram of fig. 21. The swarm of points is represented by the dotted line, which is drawn in such a way that the sum of squares of the perpendiculars from the points to this line is the smallest possible; the coefficient of correlation, being 0.722, indicates a significant correlation between the two sets of data. The deviation of the line from the ideal relation, represented by the line of equality, is only small.

It must be pointed out here that the two sets of data, correlated above, have not been obtained independently of each other. The positions

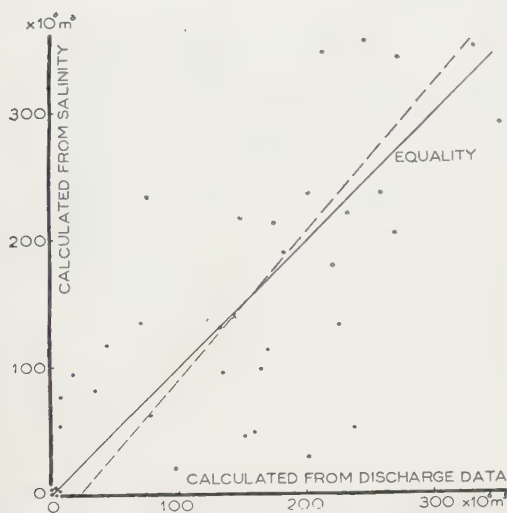


Fig. 21. The relation between figures for fresh water present in the Wadden Sea as computed from salinity measurements, and the amounts calculated directly from discharge figures.

along the horizontal axis have been found from the discharge data by means of segments. The latter, however, have in their turn been determined from average salinity figures. The positions along the vertical axis are based on the same salinity figures. Nevertheless, the reliability of the segmentation method followed is demonstrated by the fact that the dotted line nearly coincides with the ideal line. Also the significance of the correlation between the two sets of data is not lessened by the above mentioned interdependence. This correlation shows again that the method fol-

lowed gives reliable results, especially since for many individual data the cause of the deviation from the ideal line can be shown to be independent of this method. In some cases the value plotted along the horizontal is too high, because the salinity values were measured at low instead of high tide. Some other vertical values are too low, since the salinities were measured on days with strong wind, which caused an accelerated exchange of water.

It is further interesting to note that the two series of data can best be represented statistically by a straight line. This indicates that the rate of transport of fresh water is not influenced considerably by the amount of fresh water present; otherwise, a curved line would have been ob-

served. The straight line correlation fits in with the conclusion set down on p. 424 and 430.

III. DISTRIBUTION AND TRANSPORT OF SUSPENDED MATTER

In this chapter an attempt will be made to account for the presence of large quantities of suspended matter in the Wadden Sea and the quantitative variations occurring from place to place. Stress will be laid on the study of the light fraction (silt), since the latter comprises among other things organic matter and clay, which were considered to be of special interest.

A picture of the distribution of suspended matter throughout the area of investigation was formed by studying thousands of water samples. The local variations of suspended matter have been studied by measurements from anchored ships. Besides, observations have been carried out on particular distinct masses of water marked by floats.

The most interesting feature of the distribution of silt within the Wadden Sea is the existence of a gradient in silt concentration from the inlets to the interior part. In order to explain this it was necessary to give attention to details concerning the transport of the silt and to the composition of the bottom material. These subjects will therefore be treated in some detail. All this work would not have been possible without the valuable cooperation of the "*Studiedienst van de Rijkswaterstaat*".

I. TIDAL VARIATIONS OF SUSPENDED MATTER AT FIXED STATIONS

The variations in suspended matter in the Danish Wadden Sea have been studied in detail by GRY (1942). Most of his conclusions are in agreement with our own observations and therefore seem to hold for the Wadden Sea as a whole.

The quantity of material in suspension at a certain place depends in the first place on current velocity. As the current velocity varies periodically with the tide, observations had to be continued during at least one tidal cycle. The stations of observation were spread all over the southernmost part of the Wadden Sea. Their positions are indicated by numbered bold points in fig. 22. As a rule, samples were taken every half hour at three points along the vertical: just below the surface, about 1 meter above the bottom and at one third of the distance from bottom to surface. Simultaneously, the current velocity was measured with an Ott current meter suspended halfway down the

water. It is assumed that in this way the approximate average current velocity along the vertical was found.

In addition to the main stations, fig. 22 shows the positions of a number of secondary stations, where samples for the determination of suspended matter were collected just as at the main stations, but here no current measurements were carried out. These stations were situated

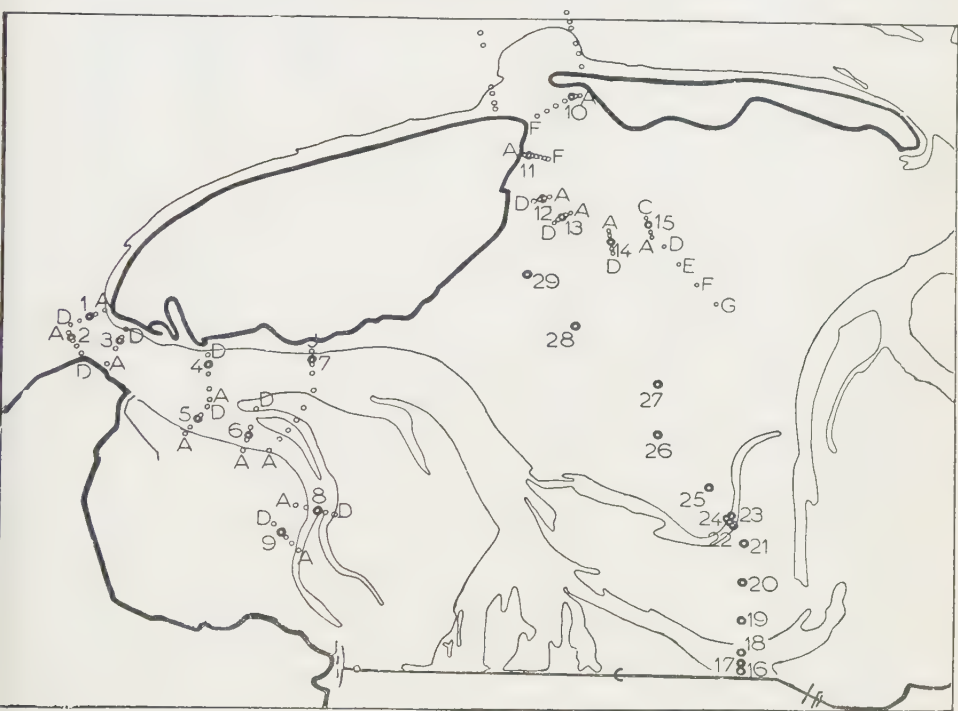


Fig. 22. Location of the stations where suspended matter was measured throughout a full tidal period; the main stations are indicated by numbered bold points, the secondary stations alphabetically; see text and table 8.

along sections running across the most important tidal channels of the area. The stations of a cross-section are marked alphabetically in addition to the number which they take from the main station situated in the same section. At the secondary stations samples were taken at intervals of 1–1.5 hours, only at the surface and near the bottom. The average quantities of silt and sand at all stations are given in table 8. Only at the main stations was sampling of sufficient frequency to allow of separation of data for flood and ebb. At most stations salinity and temperature have also been measured, but these figures will only be given if they are of importance for the problems under discussion.

TABLE 8

Average quantities of suspended matter in the Wadden Sea; for positions of stations compare fig. 22.

<i>Nr. Station</i>	<i>Date</i>	<i>Depth, HW, m</i>	<i>Flood</i>	<i>Silt, mg/l Ebb</i>	<i>Full tide</i>	<i>Flood</i>	<i>Sand, mg/l Ebb</i>	<i>Full tide</i>
1	31- 5-49	0	4.9	7.7	6.3	3.6	7.5	5.6
		6	7.6	10.3	9.0	27.6	17.4	22.5
		B, 9.5	8.5	10.0	9.3	35.8	25.9	30.4
1 A	31- 5-49	0	—	—	5.4	—	—	3.5
		B, 5	—	—	13.5	—	—	9.0
1 B	31- 5-49	0	—	—	5.6	—	—	2.8
		B, 11	—	—	13.0	—	—	7.7
1 C	31- 5-49	0	—	—	6.0	—	—	3.6
		B, 9	—	—	7.5	—	—	7.9
1 D	31- 5-49	0	—	—	5.9	—	—	4.4
		B, 6	—	—	5.7	—	—	14.0
		20	10.6	5.1	7.9	7.7	7.6	7.7
2	1- 6-49	0	4.0	3.5	3.8	3.1	2.3	2.7
		B, 32	6.9	12.6	9.8	10.9	8.1	9.5
		20	10.6	5.1	7.9	7.7	7.6	7.7
2 A	1- 6-49	0	—	—	6.1	—	—	9.4
		B, 12	—	—	10.2	—	—	8.5
2 B	1- 6-49	0	—	—	5.3	—	—	6.3
		B, 32	—	—	15.6	—	—	14.9
2 C	1- 6-49	0	—	—	6.0	—	—	4.3
		B, 30	—	—	9.0	—	—	6.0
2 D	1- 6-49	0	—	—	22.4	—	—	7.4
		B, 22	—	—	34.6	—	—	14.2
		22	9.2	8.6	8.9	48.2	31.6	39.9
3	2- 6-49	0	4.7	5.8	5.3	8.1	10.9	9.5
		B, 33	9.0	11.1	10.1	70.7	110.9	90.8
		22	9.2	8.6	8.9	48.2	31.6	39.9
3 A	2- 6-49	0	—	—	6.9	—	—	5.1
		B, 28	—	—	15.3	—	—	32.0
3 B	2- 6-49	0	—	—	5.1	—	—	4.1
		B, 39	—	—	7.8	—	—	13.0
3 C	2- 6-49	0	—	—	7.0	—	—	6.5
		B, 11	—	—	9.8	—	—	100.1
3 D	2- 6-49	0	—	—	5.7	—	—	6.0
		B, 6	—	—	11.4	—	—	20.0
		18	6.7	5.1	5.9	17.1	6.5	11.8
4	3- 6-49	0	6.8	3.5	5.2	6.6	3.9	5.3
		B, 28	9.5	6.1	7.7	42.6	21.1	31.9
		18	6.7	5.1	5.9	17.1	6.5	11.8
4 A	3- 6-49	0	—	—	4.0	—	—	2.9
		B, 10	—	—	9.6	—	—	19.8
4 B	3- 6-49	0	—	—	4.4	—	—	3.7
		B, 12	—	—	10.4	—	—	13.2
4 C	3- 6-49	0	—	—	3.9	—	—	3.0
		B, 18	—	—	5.9	—	—	12.1
4 D	3- 6-49	0	—	—	3.8	—	—	4.5
		B, 22	—	—	11.1	—	—	15.0

<i>Nr. Station</i>	<i>Date</i>	<i>Depth, HW m</i>	<i>Flood</i>	<i>Silt, mg/l Ebb</i>	<i>Full tide</i>	<i>Flood</i>	<i>Sand, mg/l Ebb</i>	<i>Full tide</i>
5	9- 6-49	0	9.3	11.8	10.6	4.7	8.5	6.6
		8	17.3	19.0	18.2	9.7	7.4	8.7
		12	41.5	29.8	35.7	13.4	11.9	12.7
5 A	9- 6-49	0	—	—	12.9	—	—	3.9
	B, 2	—	—	—	17.3	—	—	17.4
5 B	9- 6-49	0	—	—	10.2	—	—	3.0
	B, 6.5	—	—	—	23.9	—	—	5.2
5 C	9- 6-49	0	—	—	13.0	—	—	6.9
	B, 12.5	—	—	—	22.7	—	—	9.4
5 D	9- 6-49	0	—	—	14.3	—	—	25.6
	B, 6.5	—	—	—	17.9	—	—	58.2
6	10- 6-49	0	22.3	13.1	17.7	2.9	3.2	3.1
	10	14.9	21.8	18.4	2.6	3.3	3.0	3.0
	B, 16	31.3	30.5	30.9	11.1	7.8	9.5	9.5
6 A	10- 6-49	0	—	—	14.5	—	—	3.2
	B, 5	—	—	—	36.9	—	—	46.3
6 B	10- 6-49	0	—	—	11.7	—	—	2.6
	B, 12.5	—	—	—	30.8	—	—	16.6
6 C	10- 6-49	0	—	—	11.8	—	—	2.9
	B, 13.5	—	—	—	25.4	—	—	6.0
6 D	10- 6-49	0	—	—	14.6	—	—	7.9
	B, 3	—	—	—	23.8	—	—	65.0
7	11- 6-49	0	4.9	7.1	6.0	0.9	0.5	1.7
	16	7.4	10.7	9.1	2.5	1.3	1.9	1.9
	B, 24	13.0	19.1	16.1	5.8	2.9	4.4	4.4
7 A	11- 6-49	0	—	—	11.7	—	—	1.1
	B, 8	—	—	—	21.7	—	—	10.6
7 B	11- 6-49	0	—	—	12.5	—	—	1.8
	B, 12	—	—	—	25.8	—	—	11.6
7 C	11- 6-49	0	—	—	15.1	—	—	1.6
	B, 7	—	—	—	26.9	—	—	2.3
7 D	11- 6-49	0	—	—	17.4	—	—	3.1
	B, 9	—	—	—	16.0	—	—	4.9
7 E	11- 6-49	0	—	—	7.5	—	—	1.6
	B, 3	—	—	—	6.2	—	—	1.5
7 F	11- 6-49	0	—	—	7.3	—	—	1.6
	B, 7	—	—	—	18.0	—	—	3.7
7 G	11- 6-49	0	—	—	7.8	—	—	0.7
	B, 20	—	—	—	14.2	—	—	5.2
7 H	11- 6-49	0	—	—	12.3	—	—	1.2
	B, 27	—	—	—	15.1	—	—	3.7
7 J	11- 6-49	0	—	—	10.2	—	—	1.4
	B, 9	—	—	—	15.9	—	—	4.3
8	13- 6-49	0	22.7	14.7	18.7	3.2	2.9	3.1
	9	28.6	25.8	27.2	9.3	4.7	7.0	7.0
	B, 14	36.1	31.3	33.7	24.0	4.1	14.1	14.1
8 A	13- 6-49	0	—	—	20.1	—	—	3.4
	B, 7.5	—	—	—	28.2	—	—	20.8
8 B	13- 6-49	0	—	—	15.1	—	—	4.0
	B, 6.5	—	—	—	29.1	—	—	5.2

<i>Nr. Station</i>	<i>Date</i>	<i>Depth, HW, m</i>	<i>Flood</i>	<i>Silt, mg/l Ebb</i>	<i>Full tide</i>	<i>Flood</i>	<i>Sand, mg/l Ebb</i>	<i>Full tide</i>
8 C	13- 6-49	0	—	—	12.1	—	—	1.7
		B, 7	—	—	30.0	—	—	4.4
8 D	13- 6-49	0	—	—	9.6	—	—	1.3
		B, 2.5	—	—	15.7	—	—	1.5
9	14- 6-49	0-7	± 25	—	± 25	± 2	± 2	± 2
9 A	13/14-6-49	0	—	—	19.0	—	—	3.7
		B, 7	—	—	23.0	—	—	17.6
9 B	13/14-6-49	0	—	—	21.0	—	—	6.0
		B, 6.5	—	—	24.1	—	—	5.1
9 C	13/14-6-49	0	—	—	11.3	—	—	1.9
		B, 2	—	—	20.9	—	—	6.3
9 D	13/14-6-49	0	—	—	16.0	—	—	3.3
		B, 2	—	—	38.2	—	—	7.7
10	19- 8-49	0	12.7	12.7	12.7	7.7	12.7	10.2
		10	14.9	12.9	13.9	11.6	12.9	12.3
		B, 15	17.4	15.4	16.4	17.6	15.4	16.5
10	22- 8-49	0	16.9	10.7	13.8	3.0	5.1	4.1
		10	16.6	13.3	14.9	7.4	4.0	5.7
		B, 16	14.2	12.8	13.5	16.5	5.6	—
10 A	19- 8-49	0	—	—	11.8	—	—	2.6
		B, 2	—	—	14.7	—	—	11.8
10 B	19- 8-49	0	—	—	20.0	—	—	5.8
		B, 15	—	—	12.2	—	—	9.8
10 C	19- 8-49	0	—	—	13.2	—	—	4.0
		B, 2	—	—	22.3	—	—	9.3
10 D	19- 8-49	0	—	—	12.1	—	—	4.6
		B, 2	—	—	16.5	—	—	6.5
10 E	19- 8-49	0	—	—	16.7	—	—	11.9
		B, 4.5	—	—	16.9	—	—	6.0
10 F	19- 8-49	0	—	—	16.0	—	—	6.9
		B, 2.5	—	—	18.5	—	—	10.0
11	18- 8-49	0	11.8	10.4	11.1	4.5	5.4	5.0
		6	13.0	16.7	14.9	6.9	6.4	6.7
		10	17.2	16.3	16.8	7.6	20.8	14.2
11 A	18- 8-49	0	—	—	12.5	—	—	6.6
		B, 6	—	—	15.5	—	—	7.9
11 B	18- 8-49	0	—	—	13.8	—	—	23
		B, 6	—	—	15.1	—	—	30.7
11 C	18- 8-49	0	—	—	11.1	—	—	9.3
		B, 14	—	—	14.8	—	—	5.1
11 D	18- 8-49	0	—	—	13.3	—	—	6.3
		B, 2.5	—	—	15.2	—	—	7.9
11 E	18- 8-49	0	—	—	13.3	—	—	3.4
		B, 2.5	—	—	14.3	—	—	6.8
11 F	18- 8-49	0	—	—	15.1	—	—	5.3
		B, 4	—	—	13.9	—	—	16.1
12	20- 8-49	0	15.7	10.8	13.2	2.8	4.3	3.1
		5	12.4	13.9	13.2	7.6	5.8	6.7
		B, 8	20.4	13.4	16.9	10.8	9.5	10.2

<i>Nr. Station</i>	<i>Date</i>	<i>Depth, HW, m</i>	<i>Flood</i>	<i>Silt, mg/l Ebb</i>	<i>Full tide</i>	<i>Flood</i>	<i>Sand, mg/l Ebb</i>	<i>Full tide</i>
12 A	20- 8-49	0	—	—	11.0	—	—	6.0
		B, 3.5	—	—	14.6	—	—	9.2
12 B	20- 8-49	0	—	—	12.0	—	—	3.9
		B, 6	—	—	14.4	—	—	8.6
12 C	20- 8-49	0	—	—	10.8	—	—	4.9
		B, 6.5	—	—	13.9	—	—	8.5
12 D	20- 8-49	0	—	—	9.8	—	—	5.0
		B, 3	—	—	13.8	—	—	5.3
13	23- 8-49	0	14.0	9.0	11.5	12.5	4.0	8.3
		4	12.0	13.5	12.8	7.0	9.0	8.0
		B, 7	17.0	19.5	18.3	7.5	12.0	9.8
13 A	23- 8-49	0	—	—	9.6	—	—	3.7
		B, 5	—	—	18.6	—	—	21.8
13 B	23- 8-49	0	—	—	9.3	—	—	3.8
		B, 6	—	—	14.2	—	—	18.4
13 C	23- 8-49	0	—	—	10.1	—	—	2.8
		B, 6.5	—	—	13.4	—	—	10.3
13 D	23- 8-49	0	—	—	10.5	—	—	3.3
		B, 5.5	—	—	11.0	—	—	15.6
14	24- 8-49	0	49.5	61.5	55.5	7.8	21.5	14.7
		3	46.5	58.0	52.3	50.7	118.1	84.4
		B, 6	66.5	59.5	63.0	81.0	—	—
14 A	24- 8-49	0	—	—	36.3	—	—	12.0
		B, 3	—	—	36.8	—	—	45.2
14 B	24- 8-49	0	—	—	38.7	—	—	10.8
		B, 5	—	—	41.2	—	—	31.2
14 C	24- 8-49	0	—	—	32.0	—	—	8.0
		B, 5	—	—	37.9	—	—	24.6
14 D	24- 8-49	0	—	—	31.9	—	—	6.6
		B, 4	—	—	46.9	—	—	57.6
15	25- 8-49	0 (B, 9.5)	24.8	13.0	18.9	5.0	4.3	4.7
15 A	25- 8-49	0	—	—	19.9	—	—	3.2
		B, 4	—	—	35.5	—	—	53.2
15 B	25- 8-49	0	—	—	30.0	—	—	10.4
		B, 10	—	—	47.1	—	—	13.7
15 C	25- 8-49	0	—	—	36.2	—	—	31.4
		B, 2.5	—	—	42.6	—	—	45.9
15 D	25- 8-49	0	—	—	16.8	—	—	6.5
15 E	25- 8-49	0	—	—	16.8	—	—	4.3
15 F	25- 8-49	0	—	—	12.1	—	—	2.9
15 G	25- 8-49	0	—	—	11.9	—	—	3.1
16	22- 5-51	0	24.7	21.0	45.7	6.3	4.8	11.1
		B, 4.5	23.8	27.2	51.0	11.8	6.0	17.8
17	22- 5-51	0	14.0	14.3	28.3	6.6	5.8	12.4
		B, 8	35.5	30.1	65.6	7.9	7.6	15.5
18	22- 5-51	0	7.6	7.1	14.7	5.5	4.1	9.6
		8	11.6	11.0	22.6	8.5	8.8	17.3
		B, 14	13.9	11.9	25.8	17.1	6.6	23.7
19	5- 6-51	0	19.3	12.0	31.3	7.1	4.1	11.2
		B, 2	19.5	12.6	32.1	4.4	4.3	8.7

<i>Nr. Station</i>	<i>Date</i>	<i>Depth, HW, m</i>	<i>Flood</i>	<i>Silt, mg/l Ebb</i>	<i>Full tide</i>	<i>Flood</i>	<i>Sand, mg/l Ebb</i>	<i>Full tide</i>
20	5- 6-51	0	13.9	8.1	22.0	7.8	3.3	11.1
		B, 2	20.5	9.4	29.9	10.2	5.6	15.8
21	5- 6-51	0	12.7	7.7	20.4	4.9	4.9	9.8
		B, 2	13.5	8.2	21.7	9.7	4.9	14.6
22	25- 5-51	0	11.7	9.2	20.9	5.0	4.9	9.9
		B, 11	20.1	11.6	31.7	19.2	9.5	28.7
23	24- 5-51	0	13.3	11.0	24.3	6.3	4.7	11.0
		7	18.3	16.1	34.4	6.3	5.9	12.2
		B, 11	19.8	15.8	35.6	7.4	6.3	13.7
23	25- 5-51	0	13.9	12.3	26.2	3.0	5.4	8.4
		8	18.8	15.5	34.3	6.6	4.7	11.3
		B, 12	18.2	17.3	35.5	10.4	6.1	17.5
24	24- 5-51	0	15.1	12.0	27.1	5.2	5.1	10.3
		B, 3	40.2	24.1	64.3	12.1	17.8	29.9
25	6- 6-51	0	13.7	11.4	25.1	5.4	3.8	9.2
		B, 1	—	13.8	—	—	9.7	—
26	6- 6-51	0	10.7	11.4	22.1	4.3	3.7	8.0
		B, 4.5	14.8	18.0	32.8	10.1	8.8	18.9
27	6- 6-51	0	8.2	11.8	20.0	4.6	3.6	8.2
		B, 2	13.8	15.1	28.9	3.8	5.1	8.9
28	3- 7-51	0(B, 1)	13.6	9.0	22.6	6.3	8.0	14.3
29	3- 7-51	0	13.4	16.6	30.0	9.1	9.0	18.1
		B, 1	23.3	—	—	9.9	—	—

Observations were carried out at so many points in order to gain an insight into the geographical distribution of suspended matter in the area studied. However, the variations in the quantity of suspended matter at any particular point in the course of the tide will be examined first. Three stations, numbered 3, 8 and 13, will be taken as examples. The variables measured are plotted in figs. 23, 24 and 25 respectively. The diagrams show water level, current velocity and suspended material. The rate of transport of water along the main stations, expressed in kilometers, is given in table 10 A.

The quantity of particulate matter goes up and down with the current velocity, although changes are sometimes very irregular. A strong current brings more material into suspension than a weak one. Evidently, there is constant competition between the turbulent action of the current which causes an upward movement of suspended matter, and the force of gravity which causes the particles to settle. It is understandable that the concentration of sand and silt decreases upward along the vertical, and also that this is more the case with the heavier sand grains than with the lighter silt particles (see table 8).

The suspended matter reacts with a certain inertia to changes of current velocity. Mostly, there is a lag of time between the turn of the tide, when current velocity is zero, and the moment at which the

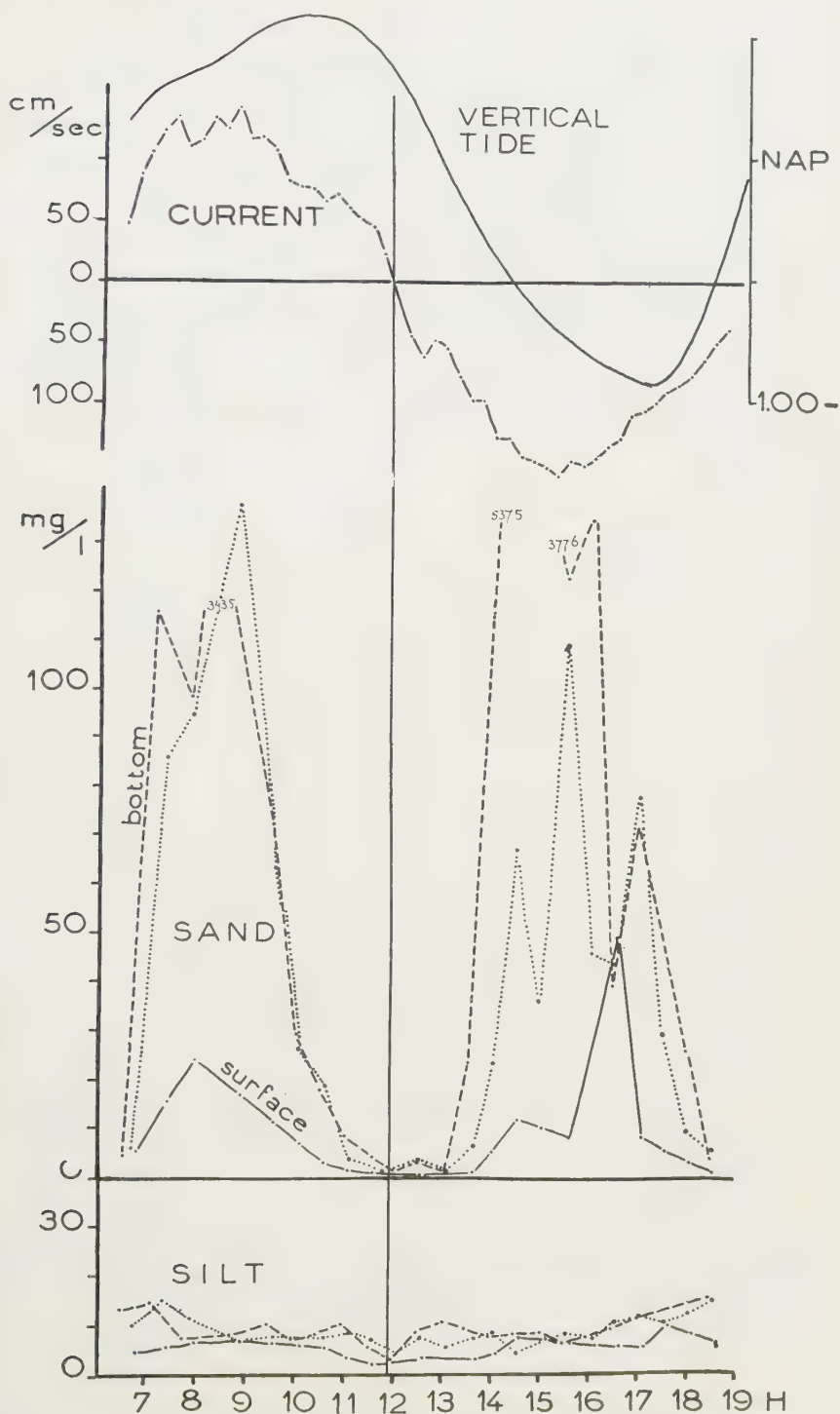


Fig. 23. Vertical and horizontal tide, and suspended matter at station 3 of fig. 22.

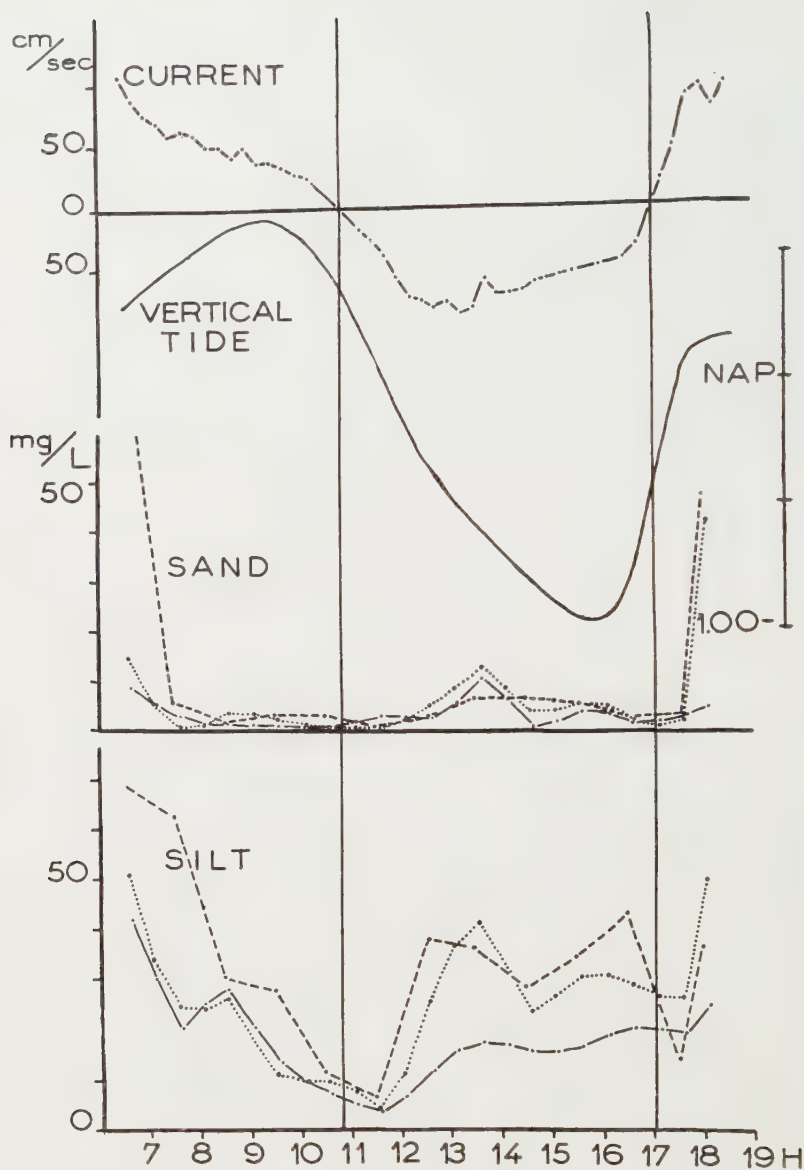


Fig. 24. Vertical and horizontal tide, and suspended matter at station 8 of fig. 22.

lowest figures for suspended material, especially suspended silt, are found. Of the three figures 23, 24 and 25, only fig. 24 shows the effect clearly; the minimum of suspended silt is in this case found from half

an hour to one hour after the turn of the tide. Table 9 gives all other observations available, which point to the same phenomenon; GRV (1942) also gives a number of examples.

The effect has not been observed at station 3 of fig. 22 and other stations with low silt concentrations, probably because the rise and fall of the curve for suspended matter in the course of the tide is slight and the minimum therefore hardly distinct. At station 13 (fig. 25) and a number of similar stations the effect is probably indiscernible because of the irregular variations in the quantity of suspended matter.

The time lag observed can easily be explained from the fact that in a period of increasing current velocity some time is needed to bring material into suspension. On the other hand, when the current decreases, it takes time before the material has settled. In an area with alternating currents an equilibrium is therefore never attained.

In this connection it is of importance to consider the rate at which

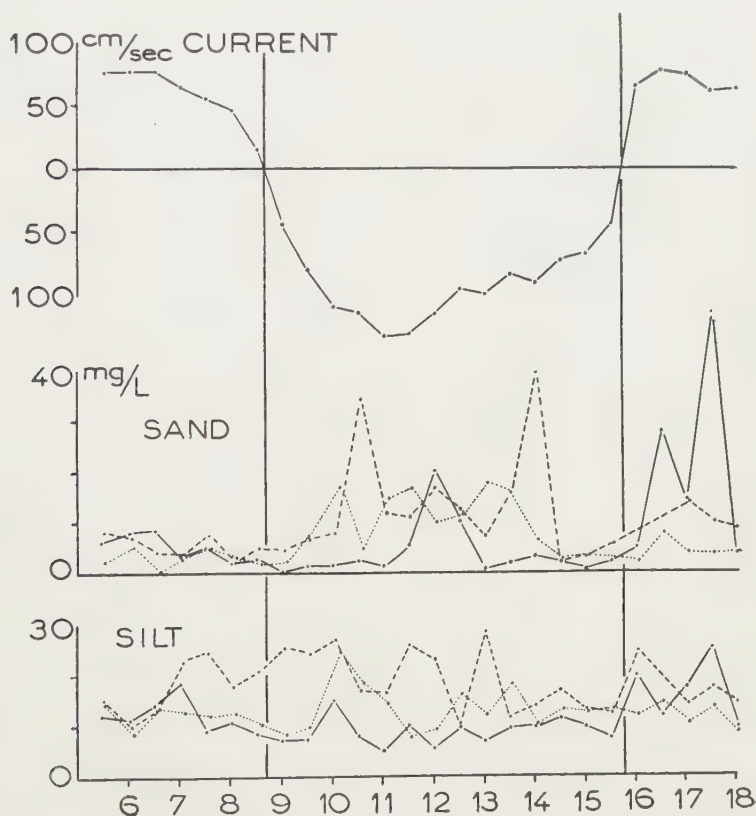


Fig 25. Current velocity and suspended matter at station 13 of fig. 22.

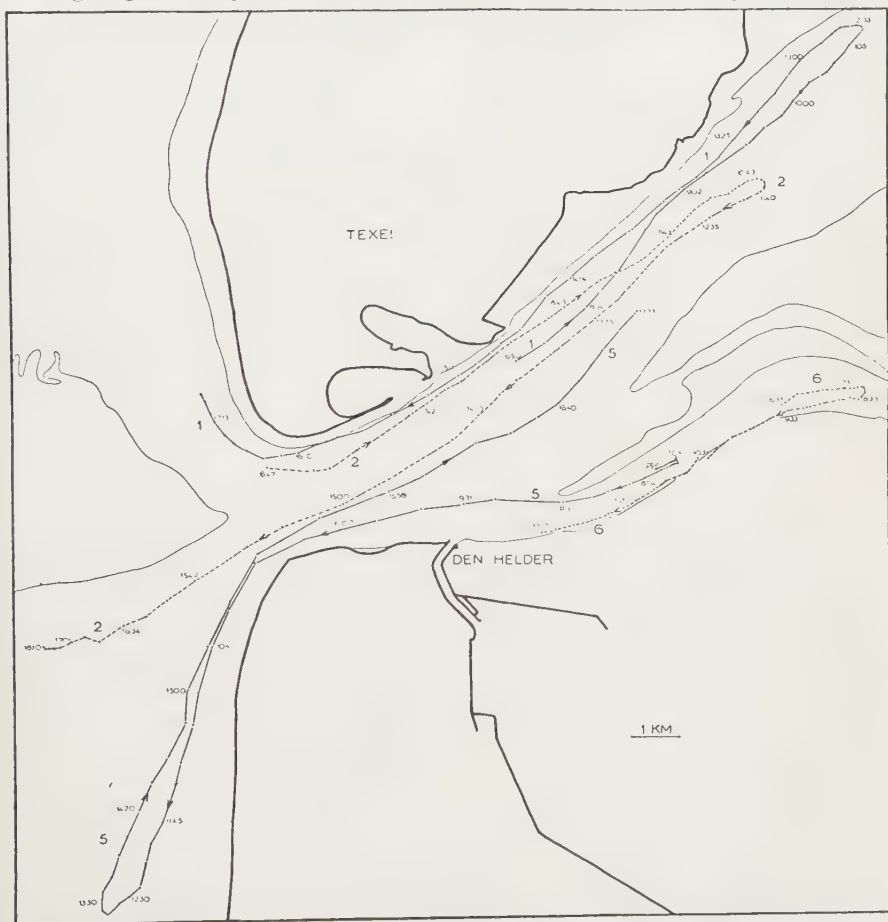
TABLE 9

The time interval separating the moment of minimum concentration of suspended matter from the turn of the tide. S D: turbidity measurement with Secchi disc.; S: concentration of suspended matter near surface. At the stations of fig. 22, not mentioned in this table, the time interval was indistinct.

<i>Date</i>	<i>Position of Station</i>	<i>Depth, m</i>	<i>Tide</i>	<i>Method of observation</i>	<i>Time interval, minutes</i>
26-6-36	Texelstroom	31	HW	S D	15
23-9-36	Marsdiep	39	HW	S D	20
23-6-39	Den Helder, harbour	10	HW	S D	20
5-6-40	Den Helder, harbour	10	HW	SD, S	25, 15
20-5-47	Texelstroom	35	HW	S D	40
20-5-47	Texelstroom	35	L W	S D	indistinct
21-5-47	Texelstroom	35	HW	S D	45
21-5-47	Texelstroom	35	L W	S D	indistinct
30-6-47	Den Helder, harbour	10	HW	S D	25
21-7-47	Den Helder, harbour	10	HW	S D	35
26-6-48	Mal Zwin	12	HW	S D	more than 40
14-7-48	Den Helder, harbour	10	HW	S D	35
6-8-48	Mal Zwin	12	HW	S D	20
6-8-48	Mal Zwin	12	L W	S D	15
23-9-48	Oude Vlie	8	HW	S D	30
21-3-49	Den Helder, harbour	10	HW	S	45
10-6-49	Mal Zwin, station 6, fig. 22	16	L W	S	30
11-6-49	Texelstroom, station 7	24	HW	S	15
13-6-49	Mal Zwin, station 8	14	HW	S	45
13-6-49	Mal Zwin, station 8	14	L W	S	30
14-6-49	Amsteldiep, station 9	7	HW	S	30
28-6-49	Mal Zwin	12	HW	S D	45
6-7-49	Den Helder, harbour	10	HW	S D	25
7-7-49	Den Helder, harbour	10	HW	S D	10
19-8-49	Engelsmangat, station 10, fig. 22	15	L W	S	30
19-8-49	Engelsmangat, station 10, fig. 22	15	HW	S	45
18-8-49	Vogelzwin, station 11	10	HW	S	± 40
19-8-49	Vogelzwin, station 11	10	L W	S	± 30
20-8-49	Vogelzwin, station 12	8	L W	S	30
20-8-49	Vogelzwin, station 12	8	HW	S	indistinct
23-8-49	Vogelzwin, station 13	7	HW	S	35
23-8-49	Vogelzwin, station 13	7	L W	S	0
25-8-49	Jack IJst, station 15	9.5	HW	S	30
25-8-49	Jack IJst, station 15	9.5	L W	S	0
17-7-50	Den Helder, harbour	10	HW	SD, S	25, 15
22-5-51	Dove Balg, station 16, fig. 22	4.5	HW	S	40
22-5-51	Dove Balg, station 16, fig. 22	4.5	L W	S	0
22-5-51	Dove Balg, station 18, fig. 22	14	HW	S	60?
24-5-51	Omdraai, station 23	11	HW	S	50
25-5-51	Omdraai, station 23	12	HW	S	30
6-6-51	Binnen Breesem, station 26	4.5	HW	S	20
6-6-51	Binnen Breesem, station 27	4.5	L W	S	indistinct
28-6-51	Texelstroom	35	L W	S D	30

the suspended particles settle. Though sand grains up to $200\ \mu$ have been observed under the microscope in small numbers, the average grain size of the sand will probably not have surpassed $100\ \mu$. According to Stokes' law sand grains of $100\ \mu$ diameter sink about $0.5\ \text{m/min.}$; sand grains of $50\ \mu$ about $0.1\ \text{m/min.}$ On an average, the silt fraction, consisting of particles smaller than $50\ \mu$, may sink some $1\text{--}10\ \text{cm/min.}$ During slack water the sand fraction will therefore settle out of the upper part of the water column within a few minutes. The silt fraction will need much more time. Hence it is primarily silt which causes the interval in time between the turn of the tide and the moment of minimum concentration of suspended matter.

Figs 23 and 24 show that the silt concentration is higher at low



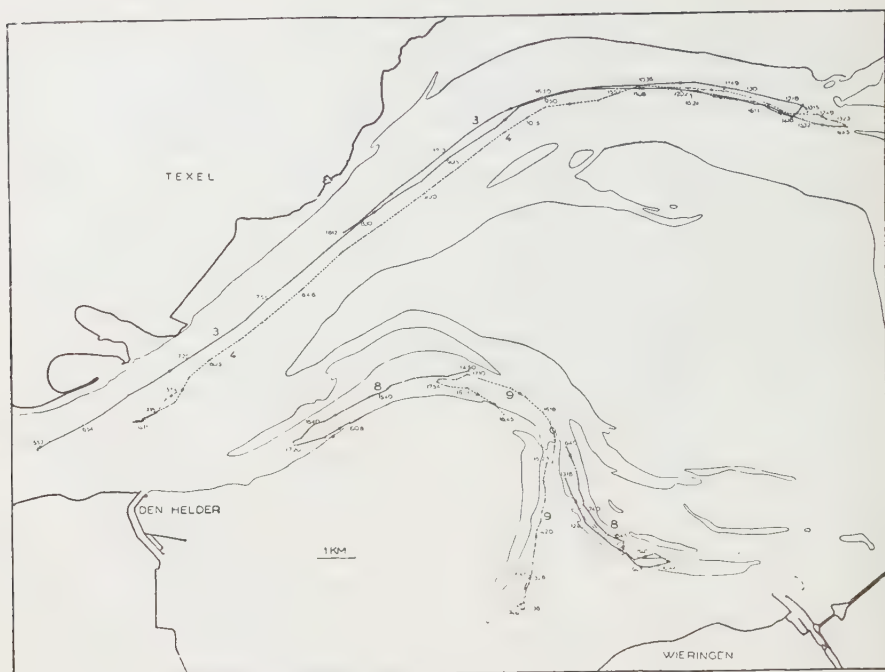


Fig. 26 B

tide than at high tide. As will be shown, this difference is caused by the geographical distribution of the suspended matter, which will be discussed below.

2. OBSERVATIONS NEAR MOVING FLOATS

In the case of a fixed station, as discussed in the previous paragraph, one is concerned with samples from different water masses, since during the observations the water passes by the place of observation. Useful additional information has been obtained by taking samples from a special mass of water marked by a float. The float consists of two iron planes fastened perpendicularly to each other and hanging vertically from a wire attached to a small buoy. If the planes are large enough, the movements of the buoy depend on the velocity of the water layer in which the planes are suspended and not on the current velocity at the surface. In most experiments the planes hung in the bottom water.

The distances travelled by the floats during approximately one tidal cycle are given in figs. 26 and 27, and table 10. On the Texelstroom, the largest channel of the Marsdiep area, distances of more than 20 kilometres were covered; in the smaller channels distances were pro-

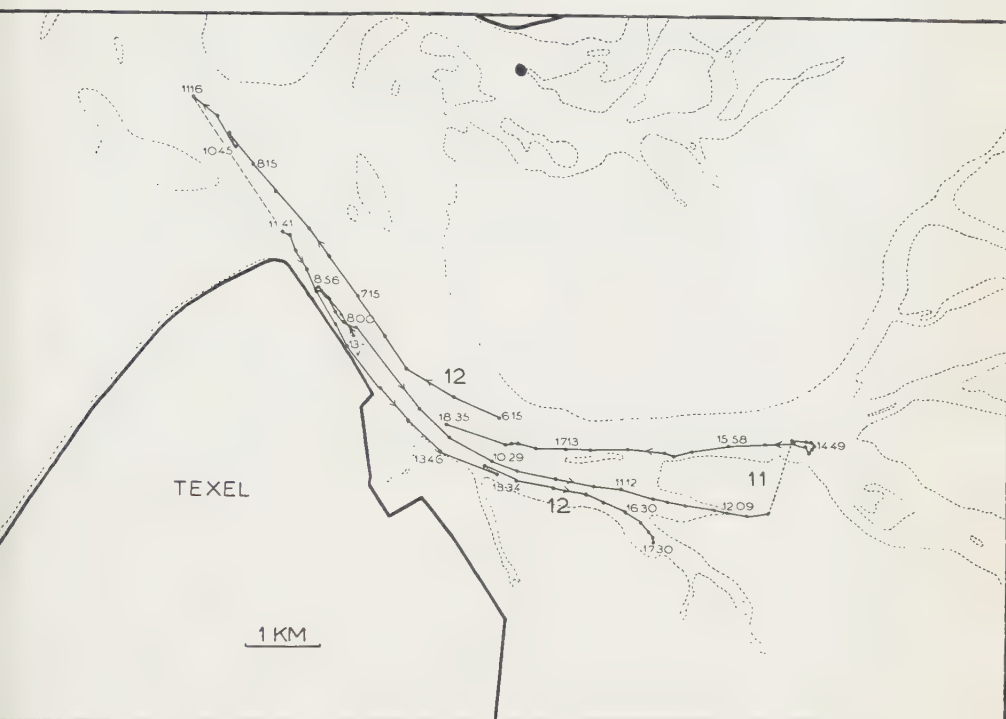


Fig. 27. Distances covered by floats during one tidal cycle; Eyerlandse Gat, August 1949.

TABLE 10
Distances covered by floats; compare figs. 26 and 27.

<i>Nr. Experiment</i>	<i>Date 1949</i>	<i>Tidal channel</i>	<i>Depth Float, m</i>	<i>Flood, km</i>	<i>Ebb, km</i>
1	31-5	Molengat-Textelstroom	10	—	19
2	1-6	Schulpegat-Textelstroom	10	—	18
3	2-6	Textelstroom	10	24	—
4	3-6	Textelstroom	10	22	—
5	9-6	Textelstroom-Schulpegat-Mal Zwin	10	—	21.5
6	10-6	Mal Zwin	6	—	—
7	11-6	Textelstroom	10	—	16.5
8	13-6	Mal Zwin	4	—	12.5
9	14-6	Mal Zwin-Amsteldiep	3	—	8.5
10	19-8	Engelsmangat-Vogelzwin	6	11	—
11	18-8	Engelsmangat-Vogelzwin	6	8	—
12	20-8	Engelsmangat	0.8-10	9	—
13	23-8	Vogelzwin	2-10	± 10	± 10

portionally shorter. The floats generally followed the same traverse forth and back; an interesting exception is the experiment of 9-6-1949. At the turn of the tide the floats turned clockwise as well as counter-clockwise.

The variations in silt content in a particular mass of water during the course of a tide are the same as the changes observed at the fixed stations (figs. 28 and 29). Much silt is brought into suspension when the force of tide is at its height, whereas shortly after slack water the concentration drops to a minimum.

3. GEOGRAPHICAL DISTRIBUTION OF THE SUSPENDED MATTER

The fixed stations were situated all over the Marsdiep area and the adjoining area of the Eyerland tidal inlet between Texel and Vlieland.

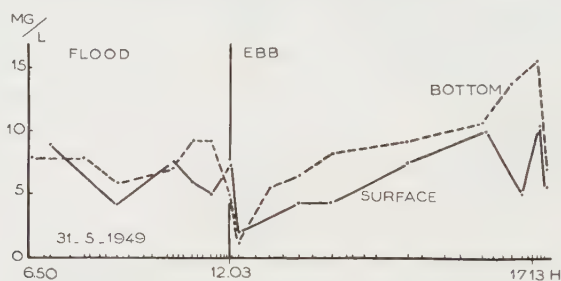


Fig. 28. Variations of suspended silt during float experiments I, fig. 26 A.

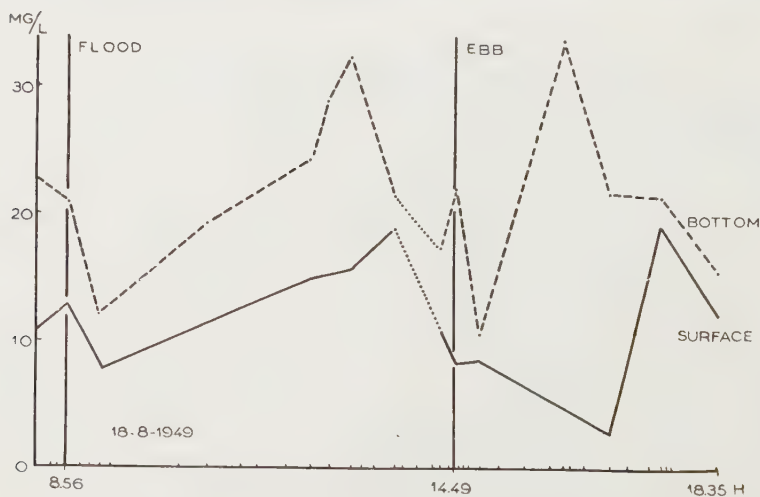


Fig. 29. Variations of suspended matter during float experiment II, fig. 27.

The observations at these stations can therefore be used to estimate differences from place to place in the amounts of suspended silt and sand. However, if comparisons between the various stations are to be valid, it must be certain that the differences observed are not caused by changes in wind force from day to day during the days of observation.

Since no special study of wind influence was made, such data are hardly available. Long-range observations, also on stormy days, would be required to gain an insight into the quantitative influence of wind. It is difficult, however, to continue measurements under bad weather conditions.

Some information about the influence of wind on the concentration of suspended matter was obtained from observations in the harbour of Den Helder. Here, measurements were made at high tide about one metre below the water surface. It must be realized, however, that the point of observation is sheltered by the coast from strong winds and therefore not representative of conditions on the open sea. Moreover, measurements were made only around the turn of the tide and therefore the concentrations measured are below the average. On the other hand, the harbour, shaped like a canal and open at both ends, formed a passage to the flats behind it and therefore fully possessed the characteristics of a tidal channel. In this respect, at any rate, it provided a good opportunity for representative sampling.

The monthly averages of the observations for the years 1949 and 1950 are given in fig. 30. The quantity of suspended material is higher in

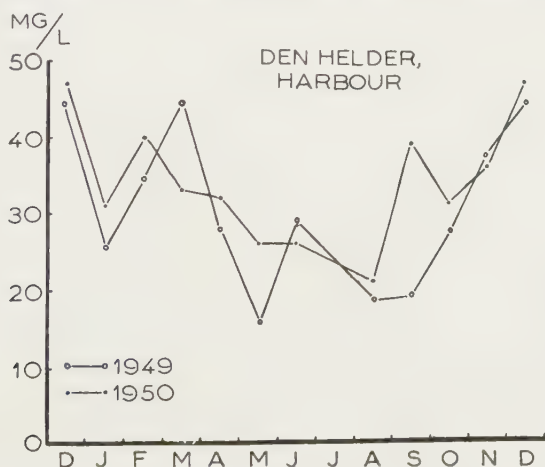


Fig. 30. Monthly averages of suspended matter in the harbour of Den Helder for the years 1949 and 1950. The samples have been taken from sea water pumped daily into the aquarium of the Zoological Station around high tide; depth about 1 m below the surface.

TABLE II

Concentration of suspended matter in the harbour of Den Helder around H W during October 1949; compare fig. 30.

Date, October	Total susp. matter mg/l	Date, October	Total susp. matter mg/l	Date, October	Total susp. matter mg/l
1	6.4	13	27.0	23	39.8
2	9.2	16	12.8	24	89.5
4	7.2	17	26.0	25	25.1
5	8.7	18	10.4	26	27.0
8	8.0	20	54.4	28	25.8
9	6.0	21	58.2	average	25.9

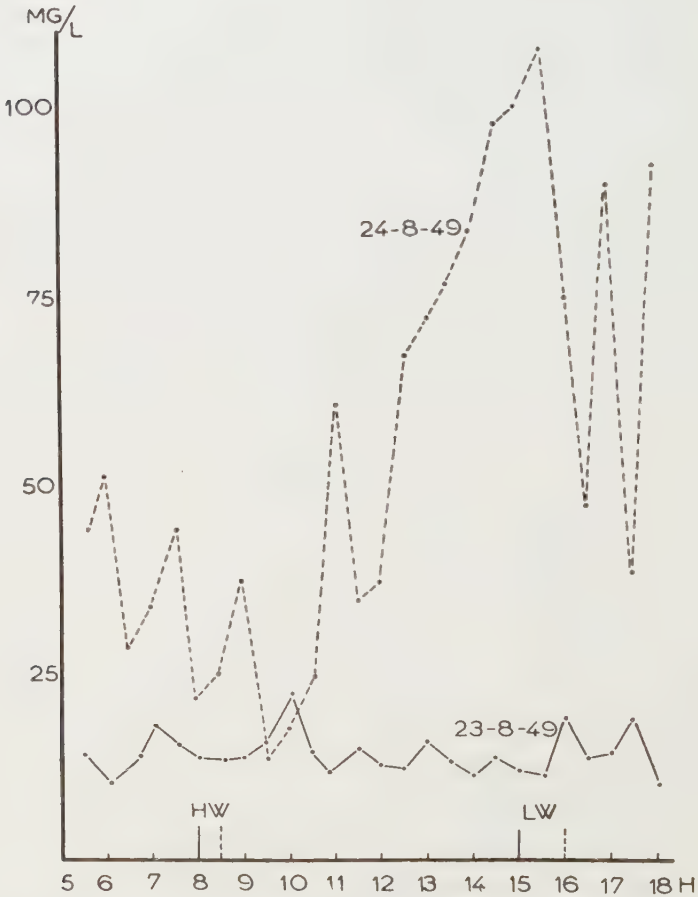


Fig. 31. Comparison of the concentration of total suspended matter at the stations 13 and 14 of fig. 22, to demonstrate wind influence; average of measurements along the vertical. Wind force resp. 7 and 12 m/sec., depth 7 and 4 m.

winter than in summer, with a maximum of about 45 mg/l in December and a minimum of 20 mg/l in August. The individual observations, however, show much larger differences; an example is given in table 11. During a heavy storm in March 1949 an exceptional quantity of no less than 447 mg/l was measured. The next day already this amount had been reduced to 20 mg/l. Obviously the higher average values in winter are not caused by a constant higher level of concentration, but by extra high values on days with strong wind. Such days occur more frequently in winter than in summer.

The observations at the main stations of fig. 22 were carried out on calm days, with the exception of those at station 14. It is interesting to compare this station with the nearby station 13, where measurements were made under normal wind conditions; in both cases the depth of the water was about the same. On the rough day the concentration of suspended matter was from 4 to 5 times as high as on the calm day (table 8; fig. 31). It is clearly to be seen that sand contributes more to this increase of concentration than the finer material does, probably because the bottom near the stations is poor in silt.

From the above observations it may be concluded that wind has an appreciable influence on the amount of material in suspension. Since most observations were carried out on calm days in summer, the average silt values found are lower than the true annual average; judging from figures obtained for the harbour of Den Helder they are perhaps even twice as low. On the other hand, the constant weather conditions during the observations increased the probability that the

TABLE 12

The average surface concentration of suspended matter in a section compared with the concentration in the same section a day or a few days later; for positions of sections compare fig. 22.

Section	First observation	mg/l	Second observation	mg/l	Difference, mg/l
2, A-D	1949, 31 May	17.3	1949, 1 June	15.3	-- 2.0
3, A-D	1 June	13.3	2 June	10.7	-- 2.6
4, A-D	2 June	8.4	3 June	7.4	-- 1.0
5, A-D	3 June	16.3	9 June	21.7	+ 5.4
6, A-D	9 June	15.7	10 June	17.3	+ 1.6
7, A-J	10 June	15.1	11 June	12.9	-- 2.2
7, A-J	11 June	12.9	13 June	14.0	+ 1.1
8, A-D	13 June	16.0	14 June	14.3	-- 1.7
11, A-F	18 August	21.7	19 August	26.3	+ 4.7
12, A-D	18 August	22.6	20 August	17.2	-- 5.4
13, A-D	20 August	17.6	23 August	13.5	-- 4.1
14, A-D	23 August	20.5	24 August	68.4	+47.9
15, A-C	24 August	60.9	25 August	43.9	--17.0

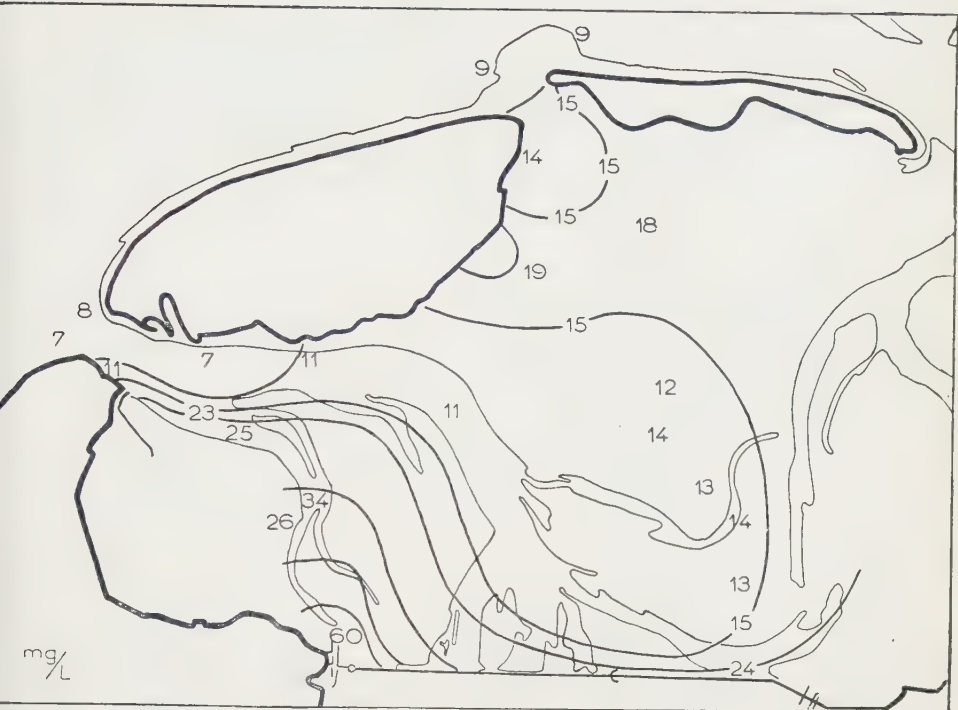


Fig. 33. Geographical distribution of silt; average concentrations, compare table 8.

lowest values observed, generally around high water at the end of the flooding tide. The average values are the arithmetic means of all figures collected at a certain station during one tidal cycle. Maximum values indicate the largest quantities of silt, mostly measured during or shortly after maximum flood or ebb current; the differences between flood and ebb maxima are mostly small. Both maximum and minimum values refer to the average concentrations along the vertical.

The geographical distribution of the average silt values shows a gradual increase of suspended silt from the North Sea inward (fig. 33). The increase is most pronounced in the direction of the coast and the Afsluitdijk. At the western end of the dike values up to 60 mg/l are found. Along the Texelstroom suspended silt increases only slowly. To give a clear picture of the distribution some isographs are drawn, but no special importance should be attached to their course.

Roughly the same pattern is found for the geographical distribution of maximum and minimum values; in the latter case the differences from station to station are very small. It may therefore be concluded

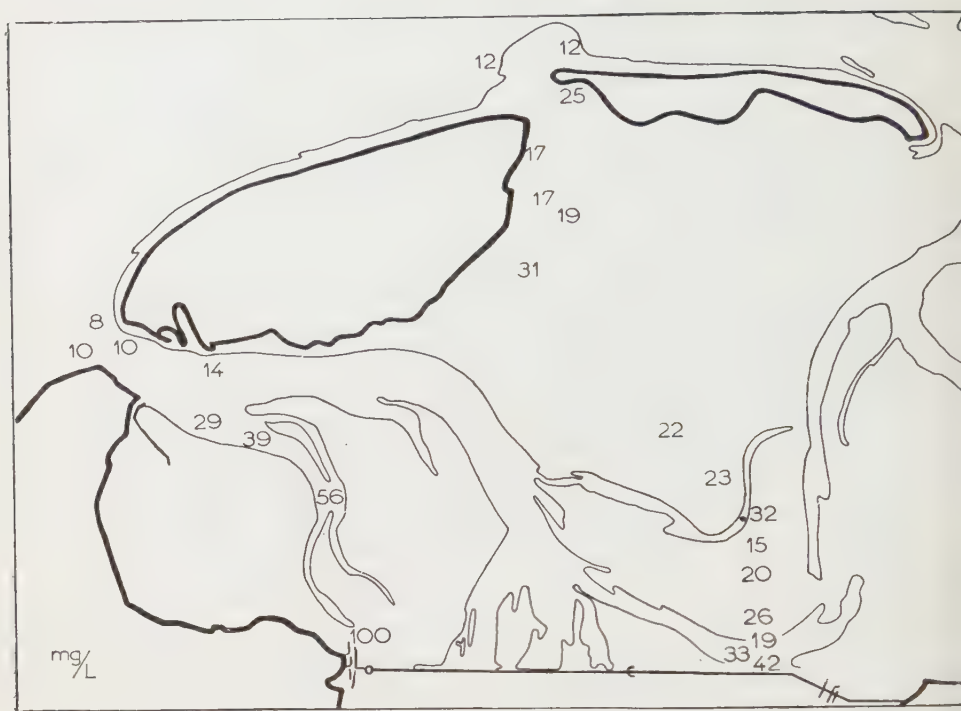


Fig. 34. Geographical distribution of silt; maximum concentrations.

that throughout the whole tide the silt concentration within the Wadden Sea is on a higher level than in the North Sea and that this concentration increases gradually in the direction of the coast.

From fig. 33 and table 8 the average concentration of suspended silt of the part of the Wadden Sea here studied has been estimated at 18 mg/l. The average concentration of sand is about 5 mg/l (see table 8), so that the total average amounts to 23 mg/l. The adjoining part of the North Sea contains only 6 mg/l of suspended silt or one third of the Wadden Sea value (see below). It has been remarked already that these values only hold for calm weather conditions.

Not only in the area dealt with in this investigation, but also in other parts of the Wadden Sea, is the silt content of the water relatively high, as appears from observations by GRY (1943) in areas near Esbjerg (Denmark) and by HAGEN (1856; compare KALLE, 1945) and LÜNEBURG (1951) for the Jade Bay. Also KAMPS (personal communication) found the same for the eastern part of the Dutch Wadden Sea.

Before we can discuss the cause of these high concentrations, it is

necessary to know the quantities of suspended silt of the surrounding areas that exchange water with the Wadden Sea. In this respect the North Sea and the IJsselmeer are of importance.

North Sea observations were carried out during calm weather in four sections perpendicular to the Dutch coast, in a section running parallel with the coast, and from the lightvessel Texel off the Marsdiep (fig. 1, table 13 and fig. 35). With the exception of those measured close

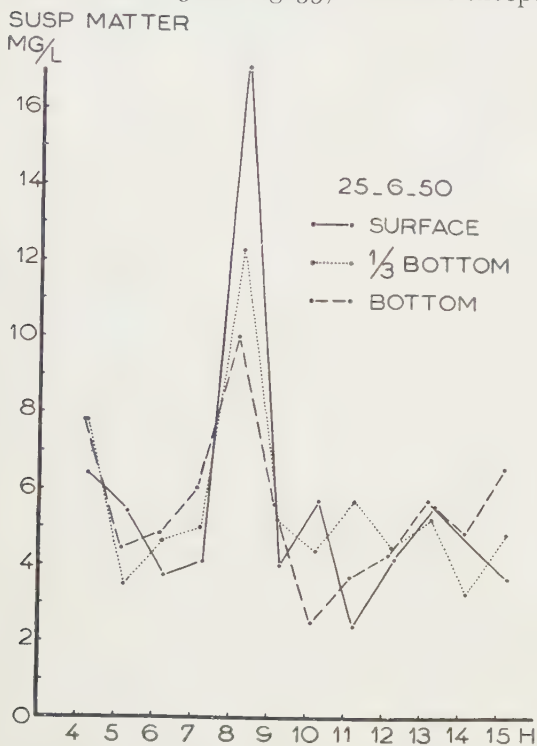


Fig. 35. Variation of total suspended matter near the Dutch lightvessel Texel; for location compare fig. 1.

18 mg/l. No quantities of sand of any importance were found in the IJsselmeer water.

by land, the values for the total of suspended matter are low. The above mentioned value of 6 mg/l has been accepted as the silt concentration of the water entering the Marsdiep.

Considerable quantities of water are further supplied to the Wadden Sea by the IJsselmeer. A number of data were collected about the fresh water discharged at Den Oever and Kornwerderzand (table 14). Suspended matter was found to vary between 10 and 30 mg/l, with an average concentration of about 15 mg/l. It will be observed that this amount lies below the average silt concentration of the adjoining part of the Wadden Sea itself and even below the over-all average of

4. TRANSPORT OF SUSPENDED SILT

For a discussion of the causes of the geographical distribution of silt observed it will be of importance to know the quantities of silt transported by the tidal currents and to determine whether there is a significant difference between the figures for ebb and flood.

TABLE 13

Total suspended matter in the North Sea near the Dutch coast; compare fig. 1.

<i>Nr. Station</i>	<i>Date</i>	<i>Latitude</i>	<i>Distance from coast in km</i>	<i>Depth, HW, m</i>	<i>Total suspended matter, mg/l</i>		<i>Remarks</i>
					<i>Surface</i>	<i>Bottom</i>	
1	23-6-49	52° 54'	2.2	8.5	7.5	16.4	Section off
2			4.8	11.5	7.9	18.0	Callantsoog;
3			7.6	18.0	7.9	8.2	average of one tide
4			10.5	19.0	5.3	7.5	
5			13.5	22.0	5.9	3.6	
6			16.2	24.5	5.5	6.6	
7	28-6-49	52° 9'	3.6	11.5	6.5	19.0	Section off
8			5.1	16.0	6.8	8.4	Wassenaar; average
9			6.5	18.5	5.1	6.8	of one tide
10			7.9	18.5	6.6	6.9	
11			9.6	19.0	4.8	5.9	
12			11.2	20.0	6.0	7.0	
13	24-6-49		8.—	—	3.8	—	11 Surface samples from Den Helder to Hook of Holland
14	22-8-48	53° 22'	0.8	3.5	9.5 (2.2)	12.8 (1.3)	Section off Vlieland;
15			1.6	3.5	10.8 (3.1)	12.0 (2.7)	average of one tide;
16			2.2	3.0	12.7 (4.1)	12.3 (2.0)	data on sand in
17			2.9	8.5	11.6 (3.1)	14.2 (2.3)	parentheses
18			3.3	15.0	10.2 (2.5)	14.7 (4.2)	
19			2.8	15.5	9.4 (2.9)	9.7 (1.9)	
20	22-8-49	53° 18'	0.4	2.0	19.9 (10.9)	26.1 (11.4)	Section off Texel;
21			0.8	2.0	15.4 (5.5)	20.5 (6.2)	average of one tide;
22			1.3	5.0	17.3 (9.4)	14.4 (4.2)	data on sand in
23			1.7	6.5	11.0 (2.9)	19.8 (5.8)	parentheses
24			3.8	11.5	6.9 (1.6)	12.1 (1.7)	
25			4.6	14.5	7.2 (3.9)	8.1 (1.8)	
26	22-9-49		8.—	—	5.0	—	9 Surface samples from Terschelling to Den Helder
27	22-6-50		13.—	22.0	8.5	16.8	Lightvessel Texel, H.W., wind force 7
27	25-6-50		13.—	22.0	5.7	6.0	Light vessel Texel, tidal average
28	26-6-50		13.—	22.0	4.5	6.0	Lightvessel Texel, H.W., wind force 1-3.

The amounts of silt passing the stations of observation during ebb and flood tide respectively can be found by multiplying the figure for silt by that for the current velocity measured simultaneously. If silt concentration is given in mg/l and current velocity in dm/sec the result can be expressed in milligrams of silt passing every second through a vertical area of one dm² perpendicular to the current.

TABLE 14

Total suspended matter in fresh water discharged from the IJsselmeer at Den Oever and Kornwerderzand around low water.

<i>Date 1950</i>	<i>Den Oever, mg/l</i>	<i>Date</i>	<i>Den Oever, mg/l</i>	<i>Kornwerderzand, mg/l</i>
1-8	17.9	4-9	—	9.9
2-8	11.7	5-9	9.7	10.1
3-8	12.6	5-9	12.9	13.3
4-8	11.7	8-9	14.3	16.5
4-8	21.0	8-9	8.0	—
5-8	15.8	9-9	9.7	21.4
5-8	11.4	11-9	10.6	29.0
7-8	9.2	12-9	8.4	22.8
8-8	10.7	12-9	—	10.0
14-8	14.3	13-9	10.4	22.9
15-8	12.8	13-9	12.2	16.5
17-8	11.9	14-9	11.3	14.5
18-8	12.2	14-9	17.0	15.7
19-8	15.2	15-9	10.5	18.6
25-8	13.1	15-9	14.6	—
26-8	14.8	18-9	18.2	24.5
28-8	14.7	19-9	—	45.0
29-8	11.1	19-9	11.6	23.5
30-8	13.3	20-9	—	17.5
30-8	12.0	20-9	15.9	32.0
31-8	11.3	21-9	17.9	22.5
31-8	17.8	22-9	18.4	17.6
1-9	12.6	23-9	13.8	14.5
		24-9	—	15.4
		24-9	18.1	13.3
		25-9	13.3	21.7
		25-9	11.1	17.1
		26-9	24.0	22.7
		26-9	14.7	18.2
		27-9	—	11.1
		27-9	12.6	14.7
		28-9	14.1	23.3
		28-9	13.6	22.6
		29-9	11.5	12.5
		29-9	16.3	17.5
		30-9	—	15.6
		30-9	12.9	13.6
		1-10	13.1	—
Average	13.5		13.5	18.8

The example given in fig. 36 is based on data regarding silt and current found in fig. 23; the vertical mean of silt concentration had to be used, because only the vertical mean of current velocity was measured. In the graph the areas enclosed by the horizontal axis and the curve therefore represent the total quantities of silt transported

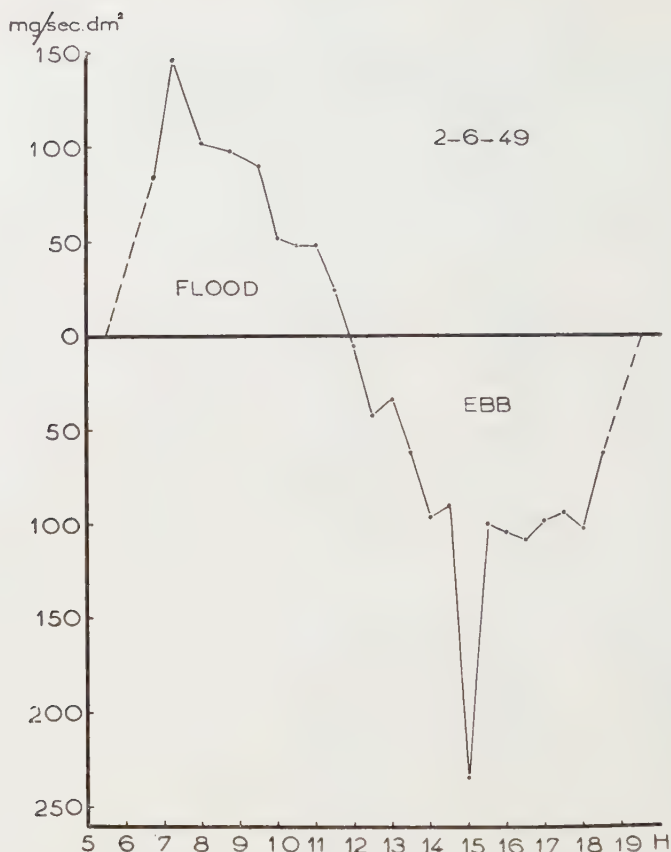


Fig. 36. Transport of silt at station 3 of fig. 22, compare also fig. 23.

through one dm^2 in flood and ebb direction respectively. The difference between the two areas represents the residual transport of silt, which in this particular case is found to be in ebb direction.

In this way the transport of silt has been calculated for most of the main stations of observation (table 15). In some cases flood transport is found to be larger than ebb transport, sometimes the reverse is the case, and a few times there is no appreciable difference. The results thus provide no general evidence for the existence of a one-sided transport of silt. Perhaps an exception must be made for some areas, for example the tidal channel Omdraai, where all observations indicate a residual transport in flood direction (stations 22, 23 and 24). This channel forms the connection between the Marsdiep tidal area and the area of the Vlie tidal inlet and a surplus of silt may therefore be transported from the former to the latter area. A cross-section of the

TABLE 15

Transport of suspended silt at the main stations; compare figs. 22 and 37, and table 8.

Nr. Station	Flood, g/dm ²	Ebb, g/dm ²	Residual transport, g/dm ²	Nr. Station	Flood, g/dm ²	Ebb, g/dm ²	Residual transport, g/dm ²
3	1620	2270	Ebb 650	16	2190	1510	Flood 680
4	1620	—	—	17	—	2450	—
5	2920	3580	Ebb 660	18	1590	1680	Ebb 90
6	4210	3720	Flood 490	19	770	1020	Ebb 250
7	—	1620	—	20	550	270	Flood 280
8	3120	3010	Flood 110	21	300	290	Flood 10
9	1060	450	Flood 610	22	2130	900	Flood 1230
10	2920	2290	Flood 630	23	1910	1690	Flood 220
11	2870	3240	Ebb 370	23	2400	1650	Flood 750
11	1730	2540	Ebb 810	24	1230	790	Flood 440
12	1220	2000	Ebb 780	25	—	410	—
13	2170	3210	Ebb 1040	26	1720	970	Ebb 750
14	5010	13220	Ebb 8210	27	—	700	—
15	—	2230	—	28	360	130	Flood 230
				29	170	240	Ebb 70

channel formed by the above-mentioned stations covers at mean water level (N.A.P.) an area of 10^6 dm², so that roughly 0.7×10^6 kg of suspended silt (dry weight) would be transported through the Omdraai to the north in every tidal period. It is possible, however, that part of this amount is transported back over the flats; compare stations 18, 19 and 26.

A comparison of table 15 with table 10 (see also fig. 37) shows that residual transport of silt is mainly caused by residual transport of water and not by a larger concentration of silt during one of the two tidal phases. This shifts the problem mainly to the question of residual water movement in the Wadden Sea. So far there is no conclusive evidence of the existence of such residual transport. On the contrary, current measurements by Rijkswaterstaat (unpublished reports of VAN VEEN, 1934, and FERGUSON, 1939) show that ebb and flood transport through the Marsdiep and Vlie tidal inlets do not differ to a significant degree. According to these observations the total transport of water through the Marsdiep by the flood tide is 0.875×10^9 m³ and by the ebb tide 0.99×10^9 m³, but the possible error of observation is considered to be too large to attach value to this difference. In the Vlie tidal inlet these values amount to 0.88×10^9 m³ for the flood and 0.85×10^9 m³ for the ebb. Our own observations on the distribution of salinity and temperature do not point to a net transport of water in one direction or the other either (compare

POSTMA, 1950). Therefore, residual transport of water, if actually existing, is considered to be of minor importance. Consequently, the same applies to the transport of silt.

The transport of silt through the Marsdiep can be roughly estimated by combining the above figures found by Rijkswaterstaat with the total average silt concentration in the transverse section of the tidal inlet (table 8, stations 3 and 3A-3D, and fig. 38). This average amounts to 8.5 mg/l; the total quantity of silt transported in ebb or flood direction may therefore amount to 8×10^6 kg.

Attention may once more be drawn here to the fact that the observations were carried out under normal wind conditions. However, especially on days with strong winds or storm, much more particulate matter is brought into suspension and transported than is normally the case. Since most strong winds blow from the south-west it is possible that this causes an over-all transport of water and silt to the north-east, that is from the North Sea to the Wadden Sea and from one part of the Wadden Sea to the other. This residual transport may quantitatively be of much importance. One might ask whether it means

a gain of silt for the Wadden Sea area. The answer must remain doubtful. The Marsdiep area will probably lose silt in this way, since North Sea water, relatively poor in suspended silt, will enter the area through the Marsdiep and water rich in silt is moved to the east.

Another effect of strong winds may be of even more importance. Although these matters are to be discussed in later chapters it may be mentioned here already that the quantity of suspended silt present in the Wadden Sea depends among other things on the rate of water exchange between the Wadden Sea and North Sea. The rate of exchange is certainly accelerated by strong winds and this will cause an extra transport of suspended silt back to the North Sea, especially since it is combined with higher concentrations of silt in suspension.

The quantity of silt supplied to the Wadden Sea by the IJsselmeer can easily be calculated since both water discharge (16.8×10^6 m³) and silt concentration (15 mg/l) are known (tables 1 and 14). It

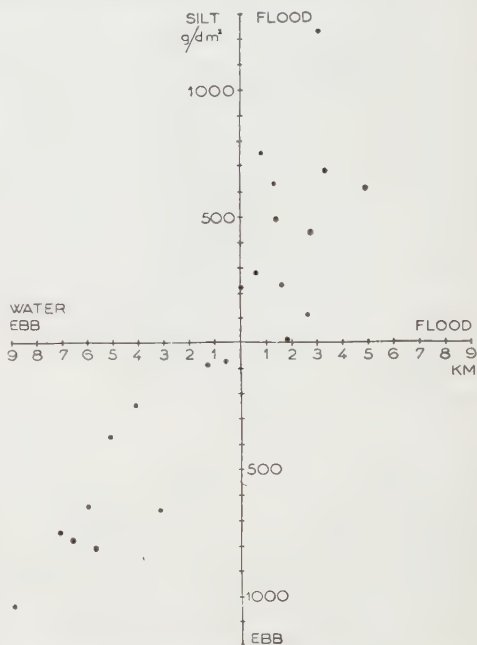


Fig. 37. Relation between the residual transport of water, expressed in km, and residual transport of silt, expressed in g/dm³, at the main stations of fig. 22.

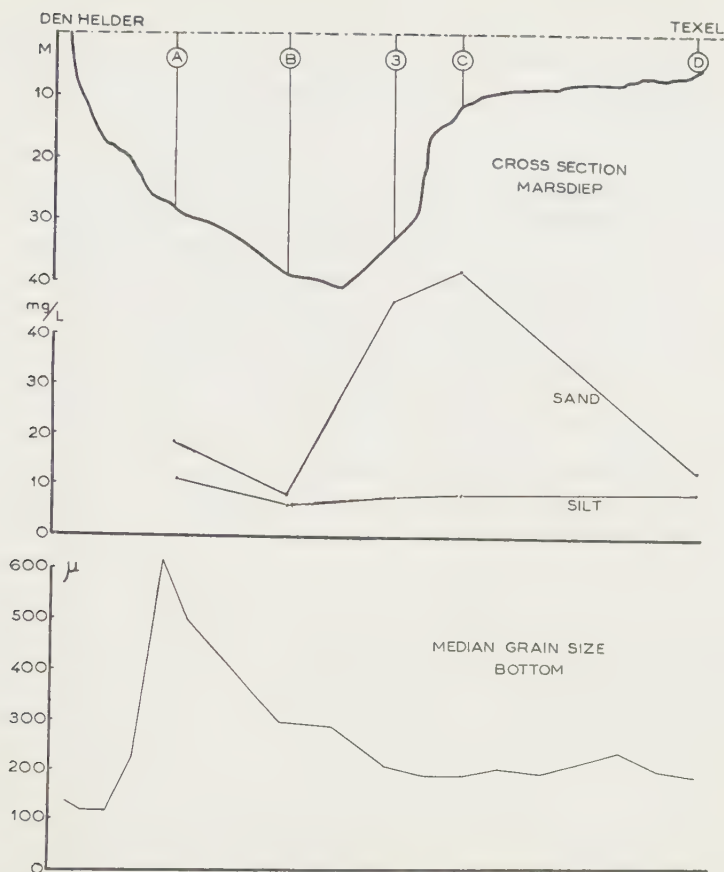


Fig. 38. Transverse section of the Marsdiep; average concentration of sand and silt (stations 3 and 2 A-3 D of fig. 22) and grain size of the bottom sediment.

amounts to 0.25×10^6 kg of silt per tide. This is a very small quantity as compared with the amounts of silt transported in the Wadden Sea itself.

So far no attention has been given to the transport of sand. Some information on this point can be obtained from the data of tables 8 and 13. The differences between individual stations as regards the concentration of sand are much larger than in the case of silt; the measurements along the cross-section of the Marsdiep may serve as an illustration (fig. 38). Obviously changes in the disposition of bottom material are greater in one place than in another; probably channels and flats become deeper at certain points and are more or less filled up at others. For example, FERGUSON (unpublished report of the „Rijkswaterstaat”, 1943) has observed that the tidal channel Molen-

gat, west of the Marsdiep, grew deeper during the period 1935-'38, while at the same time the Texelstroom, east of the Marsdiep, became shallower. This may partly be due to transport of sand from one channel to the other.

The transport of sand into the Wadden Sea has been discussed in greater detail by VAN BENDEGOM (1950), who supposes that the Wadden Sea bottom follows the rise in mean sea level, which would involve a transportation of sand from the North Sea to the flats. This sand is provided by the Dutch North Sea coast. From the rate of coastal recession during the last 100 years VAN BENDEGOM calculated that every year about 3.5×10^6 m³ of sand would be available for the western Wadden Sea. Of this amount about 1.75×10^6 m³ of sand/year or about 2.5×10^6 kg (dry weight) per tide may enter the area through the Marsdiep. The amount of water transported through this tidal inlet by ebb and flood being about 10^9 m³, a surplus concentration of 2.5 mg/l during the flooding tide would be sufficient to bring about such a movement of sand. Actually, the average concentration of sand in the water passing through the Marsdiep amounts to about 30 mg/l (table 8, stations 3 and 3A 3D, and fig. 38), so that a difference of 2.5 mg/l might easily escape observation, especially because much sand may be transported along the bottom, and therefore not be observed in sampling. Therefore the data for sand, in contrast to those for silt, have little value for transport calculations.

5. THE ACCUMULATION OF SUSPENDED SILT

It has been shown on p. 462 (figs. 32, 33 and 34) that the concentration of suspended silt in the Wadden Sea is considerably higher than in the North Sea. As the exchange of water between the two areas is intensive (see chapter II), this ought to cause a residual transport of silt along the gradient from the former area to the latter. In trying to evaluate the extent of such a residual transport we may assume that the distribution of suspended silt agrees with that of the fresh water (compare figs. 33 and 14 B). In that case during every tide about 8% of the excess of suspended silt in the Wadden Sea must be transported to the North Sea. If the surplus concentration of silt is taken to be $18 - 6 = 12$ mg/l (pp. 462 and 463), and the high tide volume of the Marsdiep area is put at 3.1×10^9 m³ (table 1), the surplus transport by the ebb movement should amount to 3×10^6 kg per tide.

It may be assumed for a moment that this amount of silt is actually transported in the course of every tide to the North Sea. In that case this loss should be neutralized by a gain from some source or other.

Since high silt concentrations are related with low salinity values, it may be asked whether the supply of silt from the IJsselmeer yields sufficient quantities. As a matter of fact, the amount of 0.25×10^6 kg per tide found on p. 469 is almost negligible if compared with the quantity of 3×10^6 kg to be accounted for. Besides, no considerable quantities of fresh water are discharged into the eastern part of the Dutch Wadden Sea, where the silt concentrations are also high.

The suggestion might be made that fresh amounts of silt are constantly brought into suspension by abrasion from the bottom of the Wadden Sea or certain sections of the coast. This appears to be the case in the Danish Wadden Sea, according to GRY (1943). However, neither extensive changes in bottom configuration nor coastal erosion take place in the Marsdiep area.

As no other sources for the supply of silt than the above-mentioned ones are available, one is led to the conclusion that eventual losses to the North Sea must be balanced by a gain from the same area. This conclusion is also supported by the observations on p. 468, which show that the amounts of silt transported through the tidal inlet by the ebb tide and the flood tide are approximately equal. As the total transport of silt during ebb or flood is 8×10^6 kg, an ebb surplus of 3×10^6 kg would most probably not have escaped observation.

If, however, no excess transport of silt to the North Sea should exist, this would mean that silt is accumulated within the Wadden Sea against its own gradient. In other words, the levelling effect of the water exchange between Wadden Sea and North Sea would be opposed by a force causing accumulation of silt, especially in the interior part of the Wadden Sea. A state of equilibrium would be reached if the two forces neutralized each other.

In this connection the following argument may be enlightening. We may for a moment assume that some dissolved, non-suspended substance is present in a higher concentration in the Wadden Sea itself than in the North Sea, for example because a surplus of the substance is temporarily introduced into the area together with the fresh water. In fact, fresh water itself may be regarded as a "negative" dissolved substance. It is self-evident that some time after the supply has been cut off, the higher concentration of the Wadden Sea will have dropped again to the concentration of the North Sea. If, therefore, such a levelling effect is not found in the case of silt, one may well ask whether this can be due to the fact that silt is not a dissolved, but a suspended substance. Contrary to the concentration of most dissolved substances, the concentration of suspended substances increases downwards from the surface to the bottom. Moreover, the concentration of the latter is subject to tidal variations (see figs. 23, 24 and 25). The accumulation

of silt may therefore either be caused by the gradient of silt along the vertical or by tidal differences in silt concentration. Both possibilities will be discussed here.

1. An increase in silt concentration from the water surface to the bottom could result in an accumulation of silt, if the bottom water were to show an over-all transport in the direction of the interior of the Wadden Sea and the surface water a similar transport in the opposite direction. This would cause a surplus transport and an accumulation of suspended silt inward. In a state of equilibrium the loss in one direction would neutralize the surplus transport in the other.

The above-mentioned circulation of water frequently occurs in estuaries, but is not found in the Wadden Sea, with the exception of the areas quite near the IJsselmeer sluices. Therefore, the explanation offered certainly does not hold for the Wadden Sea as a whole. A second objection is the existence of high silt concentrations near the Frisian coast, where no large quantities of fresh water are discharged and, consequently, no circulation of the type discussed above exists. It must therefore be concluded that the explanation suggested is not capable of general application.

Attention may be drawn here to another effect of fresh water on suspended silt. It is generally assumed that mixing of fresh and salt water causes colloidal and finely divided suspended matter to combine to particles of larger size. Such particles will settle more easily. The same accumulation of silt results from the activity of molluscs, which with their filtering mechanisms produce faecal pellets (VERWEY, 1952). These processes probably support the accumulation of silt both at the bottom and in the water, but they do not provide an explanation for the mechanism of this accumulation.

2. It may also be suggested that the transport of silt into the Wadden Sea against the gradient is in some way or other caused by the variations in silt concentration during the tidal cycle. This transport may be supposed to neutralize an equally large loss of silt in an opposite direction, caused by the water exchange in the same direction as the silt gradient.

The tidal variations of silt must then be supposed to act in such a way that the pattern of behaviour exhibited by ebb and flood in relation to silt is asymmetric, the ebb tide not being able to carry back all the silt carried inward by the flood.

In this connection attention may be drawn to fig. 39, which shows the percentages of silt in bottom samples taken by the Zoological Station for biological purposes (see also HANSEN, 1952). Unfortunately the samples are not divided equally over the area, data relating to flats being scarce. Nevertheless, the difference between the distribution of sand and that of silt is clearly brought out. This divergence is in the first place caused by the progressive decrease of water movement from

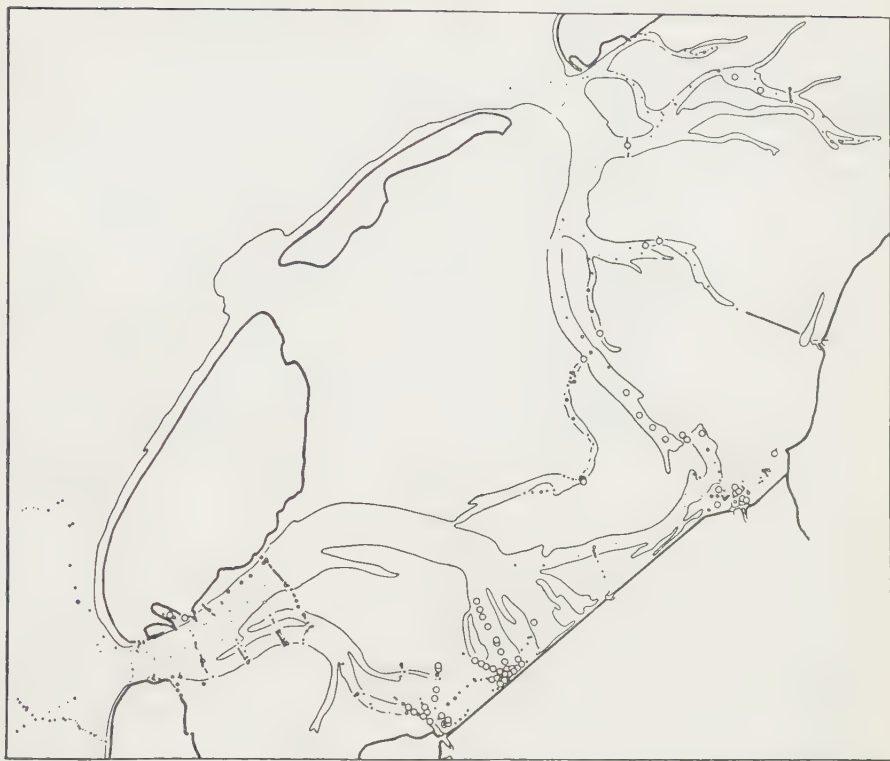


Fig. 39. Mud content of bottom samples collected with a Van Veen bottom sampler, primarily for biological research. Large circles indicate mud to half sand—half mud, smaller circles half sand—half mud to sand with little mud, smallest circles sand with very little or no mud, points coarse sand, often with gravel and shell remains.

the North Sea to the Wadden Sea interior. A soft bottom can never exist in places frequently exposed to the impact of waves or places where strong currents prevail. Silty areas are therefore restricted to flats protected against strong winds by the coast and some places near the coast too deep for the impact of waves to have any effect, and without strong currents (for example Vlieter and Amsteldiep, fig. 2).

If fig. 39 is compared with fig. 33, we are struck by the fact that the distribution of bottom silt corresponds to a notable degree with the distribution of suspended silt. The effect that creates the silt gradient may therefore also be connected with decreasing water movement from the outer to the inner part of the Wadden Sea. This point of view is also supported by the fact that the tidal flats in the eastern Dutch Wadden Sea, better sheltered from strong winds than those of the western Wadden Sea, besides being more silty, are also marked by very high quantities of suspended silt (KAMPS, personal communication).

In view of these considerations we may try to base an explanation on what we know about the inertia exhibited by suspended silt in reacting to changes of currents, discussed on p. 448–453. It has been shown that the amount of silt in suspension at each phase of a period of increasing current velocity is constantly lower than the amount found for the corresponding velocity after the steady state has been attained; during decreasing current velocity the reverse was found to be the case.

If we follow up this line of thought, the behaviour of a certain mass of water during its displacement by the flood may be studied. As long as the mass of water is travelling in the large channels, its flow is much faster than it becomes farther inward, and it contains the amount of silt appropriate to the turbulence caused by this rate of flow. More or less gradually, however, the mean current velocity decreases. The silt content being too high in relation to this slower rate of flow, part of it will slowly settle to the bottom. Because silt reacts so slowly to velocity changes, however, it will be transported farther in flood direction than would have happened if sinking took no time.

After the turn of the tide the mass of water will move in an opposite direction. However, the inert reaction of the silt to the decrease of current velocity during the transport inward has caused the silt to settle in places, where the current is actually too weak to carry it away. Therefore, if ebb and flood have about the same current velocity, a certain fraction of silt is left behind on the bottom. The latter therefore receives a second enrichment of silt above the one caused in the first instance by the decrease in water movement towards the Wadden Sea interior. The process repeats itself during every tidal period, until the bottom has become so silty, and the concentration of silt in the water overhead has become so high, that the gradient of silt thus generated neutralizes the residual transport inward.

The explanation of silt accumulation as developed above, if true, will hold for the whole of the Wadden Sea, since it is based on the progressive decrease of water movement towards the coast. In different localities, however, other forces may also play a rôle or be of even more importance. Near the mouths of the rivers Ems, Weser and Elbe, the supply of fresh water may exert a much greater influence than in the Dutch Wadden Sea and the explanation given on p. 472 may be valid. As said before, GRV (1943) has shown that in the northern part of the Danish Wadden Sea high concentrations of suspended silt are caused by erosion of coastal marshes. The same may be the case in other areas.

It may further be remarked that according to the above theory the silt gradient depends not only on the decrease in current velocity or, to put it more generally, on the decrease in water movement inward, but also on the concentration of suspended silt in the North Sea.

It may finally be observed that accumulation of silt in either the first or the second way discussed above may also occur in other estuaries than those of the Wadden Sea region. Especially the accumulation of suspended matter caused by estuarine water circulation (p. 429) may be of more widespread importance. The Nieuwe Waterweg near Rotterdam may serve as a fine example, compare CANTER CREMERS (1921). Many coastal harbours where fresh water is discharged may provide other instances.

IV. THE CYCLE OF ORGANIC MATTER

From a biological point of view organic matter constitutes the most important part of the suspended material. Sessile plants being practically absent, the production of particulate organic material by phytoplankton organisms forms the basis of animal life and determines its density. The main purpose of this chapter will be to gain an insight into this organic production.

Particulate organic matter, from a non-biological point of view, behaves as part of the suspended matter. This point will be treated in detail. Moreover, a study will be made of the seasonal variations of organic matter caused by varying rates of decomposition and production in the course of the year. Further, the exchange of organic matter between Wadden Sea and North Sea will be discussed. It will be shown that there is a residual transport of organic matter from the North Sea into the Wadden Sea. An attempt will be made to evaluate the quantitative importance of this transport and, further, to determine total phytoplankton production and mineralization of organic matter in the Marsdiep area. In this connection a study was made of the cycle of phosphorus and of chlorophyll, the former being a factor regulating production, the latter being a measure for the amount of phytoplankton.

Observations on organic matter, phosphorus components and chlorophyll were mostly carried out along the same section where also salinity data were collected (fig. 13). To supplement these observations a number of measurements were carried out in other parts of the Marsdiep area, especially in the harbour of Den Helder, which provided a convenient opportunity for daily observations. The complete data are on file at the Zoological Station.

I. QUANTITY AND COMPOSITION OF PARTICULATE ORGANIC MATTER

If suspended matter is examined under the microscope, sand grains, pieces of shells and living plankton are easily discerned. Besides these,

a relatively large amount of dead organic matter is found to be present. It will be referred to hereafter as detritus, which consists of dead organisms and all kinds of organic debris. The quantitative relation between dead and living organic matter is difficult to determine, but in the Wadden Sea the dead material certainly forms the major part, possibly up to more than 90 % of the total (p. 503). For the North Sea VAN GOOR (1923, p. 173) estimated that the aggregate of organic detritus is 50-100 times as large as the amount of plankton organisms; this value, however, may be rather inaccurate. In the Bay of Kiel more than 95 % of the particulate organic matter consists of detritus (GILL-BRIGHT, 1951), whereas in the English Channel this percentage amounts to only 15-30 % (ARMSTRONG and HARVEY, 1950, p. 151).

VERWEY (1952) assumes that the high percentage of dead organic matter present in estuarine areas is caused by the mixing of different water masses. He supposes that part of the plankton organisms are killed by sudden changes of temperature and salinity (see also BROCKMANN, 1908, 1929 and KÜHL and MANN, 1953). In addition, however, the percentage of detritus may be influenced by water movement. In deep or quiet water plankton debris may disappear from the water column because it sinks down to the bottom, whereas in shallow areas settling of detritus may to a large degree be prevented by the influence of wind and currents.

In the particular case of the Wadden Sea it is further possible that here much suspended matter, containing living as well as dead organic material, is filtered from the water through the activity of molluscs, while only dead organic matter in the form of faecal pellets is returned (VERWEY, 1952). In this way the quantity of detritus may be augmented at the expense of living organic matter, although faecal pellets are perhaps not brought into suspension easily. We shall return to these points on p. 496-498.

The chemical analyses of suspended matter have been discussed already on p. 414. Attention may be drawn here especially to the last column of table 4, giving the relation of C, N and P for the organic material. There are considerable differences in chemical composition from one sample to another, but the average of all determinations, 40:7.4:1, does not differ significantly from the relation 41:7.2:1 for living plankton (COOPER, 1934; FLEMING, 1940; KETCHUM and REDFIELD, 1949; for a summary see SVERDRUP, JOHNSON and FLEMING, 1946, p. 236; for North Sea samples compare also BRANDT and RABEN, 1920). Since it has been assumed that a large part of the organic matter consists of detritus, the relation apparently also holds for the latter, although, according to SEIWELL and SEIWELL (1938), phosphorus may be mineralized more easily than the other elements.

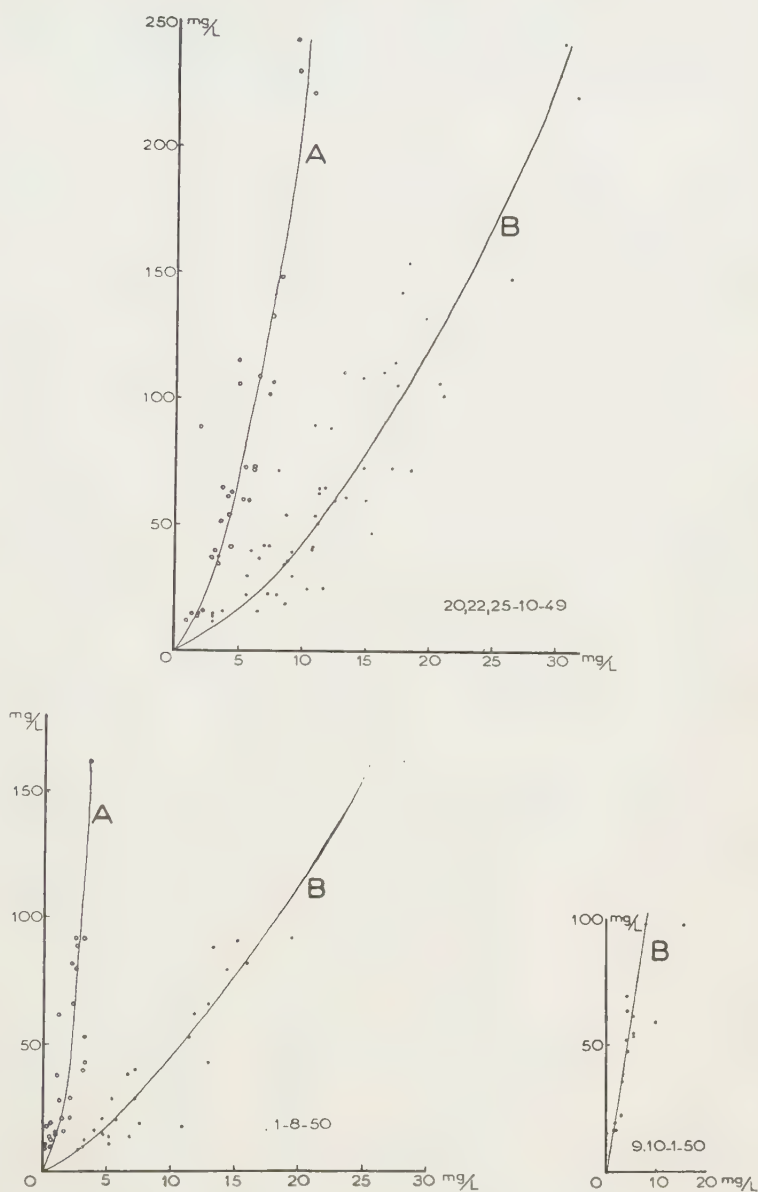


Fig. 40. Relation between total suspended matter and carbon dioxide content (A), resp. loss on ignition (B) for samples taken simultaneously along the section of fig. 13.

The amounts of organic matter present have been determined, first, by loss through ignition and, secondly, by ascertaining the quantity of particulate phosphorus. According to table 4, the phosphorus percentage amounts to about 1 % if the ratio of carbon to organic matter is put at 1:2.3. Other analyses, to be discussed below, give the somewhat lower value of 0.7 %.

2. THE RELATION BETWEEN SUSPENDED ORGANIC MATTER AND THE TOTAL AMOUNT OF SUSPENDED MATERIAL

It may be expected that particulate organic matter follows more or less closely the quantitative variations of total suspended matter. This

TABLE 16 A

Organic matter, estimated from loss on ignition minus CO₂, at the Wadden Sea stations of table 8; compare also fig. 22.

31-5-49	1	27.8	2.5	8.9	much sand
1-6-49	2	13.8	1.3	9.4	
2-6-49	3	32.2	2.6	7.8	
3-6-49	4	22.6	2.0	8.9	much sand
9-6-49	5	30.8	4.1	13.3	much sand
10-6-49	6	27.5	4.4	15.6	
11-6-49	7	13.1	2.7	20.7	
13-6-49	8	34.6	4.3	12.4	
14-6-49	9	27	3.9	14.4	only surface

TABLE 16 B

Organic matter, estimated from loss on ignition minus CO₂, at the North Sea stations of table 13; compare also fig. 1.

23-6-49	1	Surface	7.5	1.2	
		Bottom	16.4	1.4	
		Total	12.0	1.3	10.8
23-6-49	2	Surface	7.9	1.9	
		Bottom	18.0	3.5	
		Total	13.0	2.7	20.8
23-6-49	3	Surface	7.9	1.6	
		Bottom	8.2	1.5	
		Total	8.1	1.6	19.8
23-6-49	4	Surface	5.3	0.8	
		Bottom	7.5	0.8	
		Total	6.4	0.8	12.5
23-6-49	5	Surface	5.9	0.9	
		Bottom	3.6	0.9	
		Total	4.8	0.9	18.8
23-6-49	6	Surface	5.5	1.2	
		Bottom	6.6	0.8	
		Total	6.1	1.0	16.4

supposition is confirmed by observations along the section of fig. 13. The increase in total suspended matter causes an increase of its organic component, the relation between the two being best represented in most cases by a curved line, indicating that on the whole organic matter is more easily kept in suspension than the inorganic material (figs. 40 and 41).

Since it may be assumed that there is a direct correlation between the quantity of organic matter and the quantity of silt (suspended matter minus the sand fraction) the geographical distribution of organic matter will roughly correspond with the distribution of silt. If that

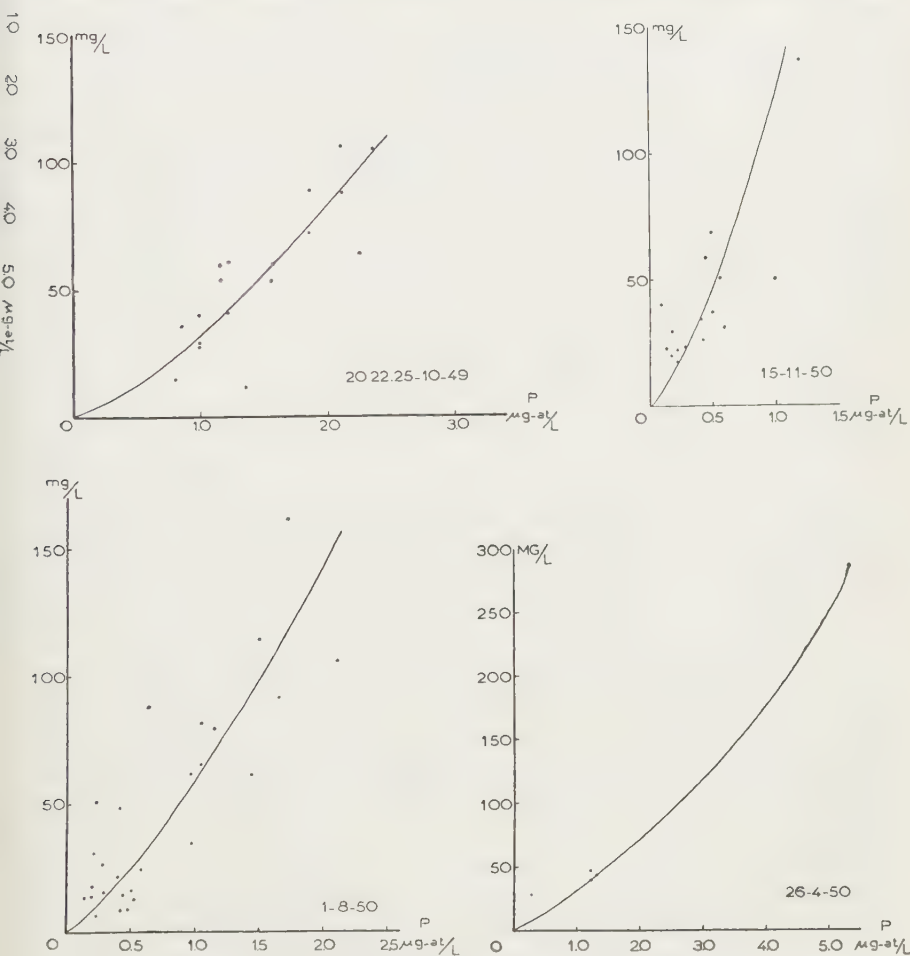


Fig. 41. Relation between total suspended matter and suspended phosphorus; compare fig. 40.



Fig. 42. The progressive increase of suspended organic matter from the North Sea to the Wadden Sea, June 1949; based on table 16.

is actually the case, the concentration of suspended organic matter of the Wadden Sea will be from two to three times higher than that of the North Sea. This is confirmed by measurements of organic matter at stations in both areas during a complete tidal period (table 16, fig. 42).

The conclusion seems justified that the concentration of suspended organic matter in the Wadden Sea is maintained at its high level in the same way as described for suspended silt in chapter III. However, in contrast to silt, organic matter is constantly in process of decomposition and synthetization. Therefore, a larger production of organic matter in the Wadden Sea itself than in the North Sea may perhaps also account for this gradient. We shall revert to this point on p. 504.

A comparison of the graphs of figs. 40 and 41 makes it seem quite probable that the amount of organic matter present changes in the course of the year. The concentration of suspended organic matter is relatively high in summer and low in winter. A more complete insight into seasonal changes is obtained by considering all the different types of observations available. Most of these observations were carried out along the section of fig. 13; a number of others refer to measurements carried out at other points of the Marsdiep area, especially in the harbour of Den Helder.

For every set of simultaneous observations the average quantities of both organic and suspended matter were determined. As the average quantity of suspended matter of the Marsdiep area is 23 mg/l (p. 462), all observations have been reduced to this mean value by means of graphs like those of figs. 40 and 41. In this way the influence of quantitative variations of suspended matter has been eliminated, and the

figures for organic matter thus will roughly represent the average amounts present. The results of the calculations are given in fig. 43, one curve showing the seasonal changes of particulate P, the other the quantitative variations of organic matter as derived from the difference between ignition loss and carbon dioxide content. The latter is assumed to be constant all the year round and therefore represented by a horizontal line, indicating the mean of the CO_2 -analyses, which is 1.8

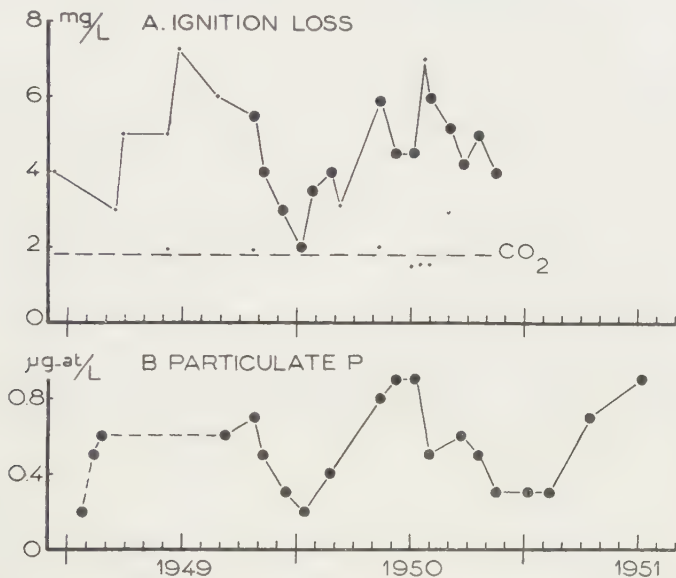


Fig. 43. Seasonal variation of organic matter (ignition loss minus carbon dioxide, A) and suspended phosphorus (B). The large points refer to observations along the section of fig. 13; the small points mainly refer to observations in the harbour of Den Helder; the CO_2 -determinations are indicated by a cross.

mg/l or 8% of the total of suspended matter. In summer organic matter is found to amount to about 4 mg/l or 17% of all suspended material, in winter it decreases to about 1 mg/l or 4%. Suspended phosphorus shows roughly the same variations. The phosphorus percentage of organic matter appears to amount to about 0.7%, which is somewhat lower than the figure derived from the analyses of table 4.

Although every single point of fig. 43 is based on a set of observations, the resulting curves derived are believed to indicate only the general trend of quantitative changes of organic matter and no special value must be attached to the position of summer maxima and winter minima.

Doubt may arise, moreover, if it is permissible to assume that the average quantity of suspended matter amounts to the same value of 23 mg/l the whole year round, because the winter averages proved to be greater than those of the summer months

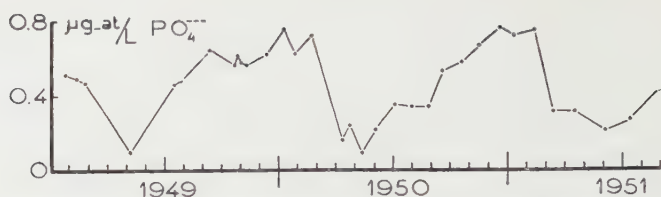


Fig. 459. Seasonal variation of phosphate in the Wadden Sea; average of the observations along the section of fig. 13.

(p. 459). However, this difference is caused by a more frequent occurrence of days with much wind during the winter months. If these days are excluded, the winter values for suspended matter are probably not very different from the summer values. Since observations were nearly always carried out under quiet weather conditions, also in winter, the summer figures are probably directly comparable with the winter figures.

So far the following conclusions can be drawn. Generally speaking, the quantity of suspended organic matter in the Wadden Sea is roughly proportional to that of suspended silt. Therefore, the distribution of organic matter is probably about the same as that of silt as shown in fig. 33 and the concentration within the Wadden Sea is high as compared with that in the North Sea. Further, suspended organic matter is subject to seasonal variations, the quantities being higher in summer than in winter.

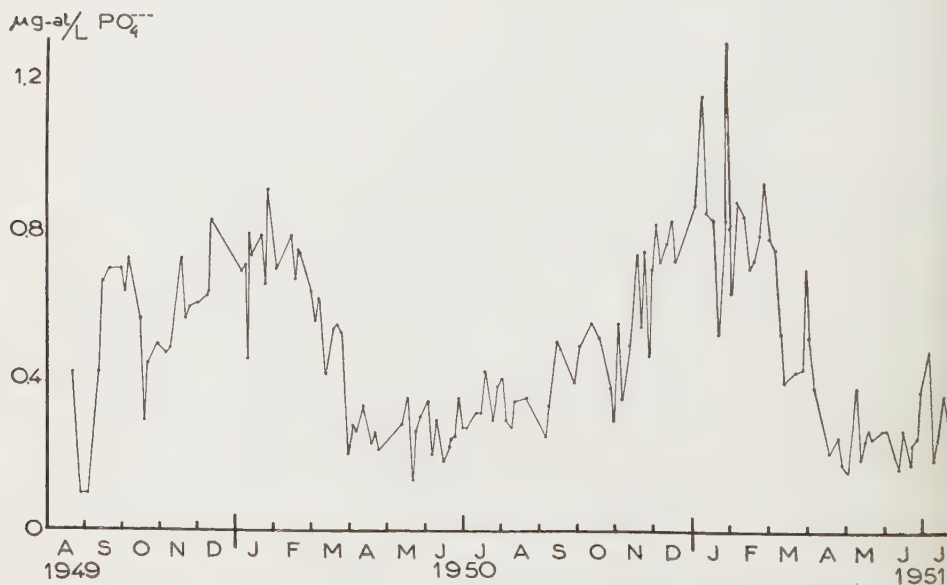


Fig. 45. Seasonal variation of phosphate in the harbour of Den Helder; observations from the water pumped daily at high tide from about 1 m below the surface into the aquarium of the Zoological Station.

3. THE CYCLE OF PHOSPHORUS

Since phosphorus is essential to the production of organic matter, more information on the cycle of organic matter may be obtained by studying the variations in the components of this element. It is present in an organic as well as an inorganic form and, besides, in a dissolved and a particulate condition. Probably, inorganic particulate P is quantitatively of minor importance, compare p. 418; thus three forms of P remain

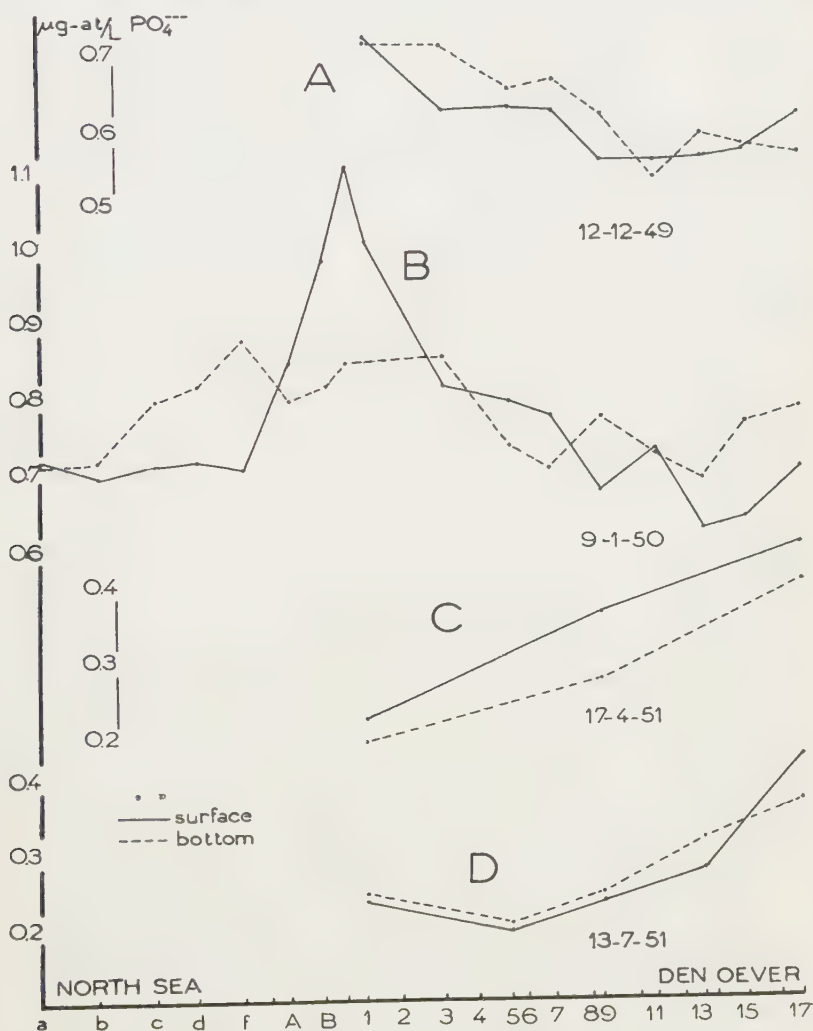


Fig. 46. Examples of the phosphate observations along the section of fig. 13.

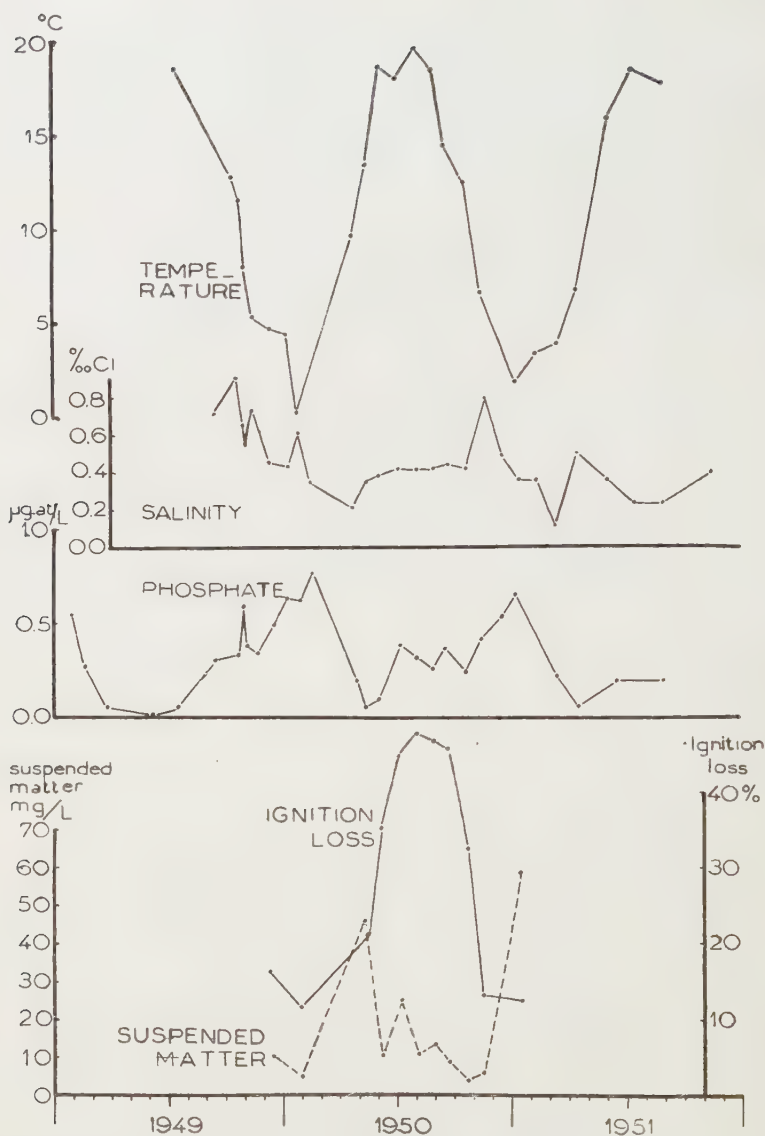


Fig. 47. Observations in the IJsselmeer near the sluices of Den Oever.

to be discussed: phosphate, dissolved organic phosphorus and particulate organic phosphorus. These three components will first be discussed separately; after that their mutual relation will be examined.

A. Phosphate

The seasonal cycle of phosphate was studied by SCHEELE and VERWEY (unpublished) from 1936 to 1940 in the harbour of Den Helder. This study was continued in 1948 and extended, moreover, over the whole of the Marsdiep area. As mentioned before, regular observations were carried out in the section of fig. 13.

Phosphate is subject to seasonal changes and shows a marked geographical distribution. The seasonal cycle of phosphate is represented in figs. 44 and 45. The annual variation corresponds with the results of similar observations carried out in other places, for example the English Channel, compare for example ARMSTRONG and HARVEY, 1950. In winter decomposition of organic matter prevails over assimilation and organic phosphorus is mineralized to phosphate; in spring and summer Wadden Sea phosphate is consumed by phytoplankton. The maximum occurs in January, the minimum in May. Evidently, phos-

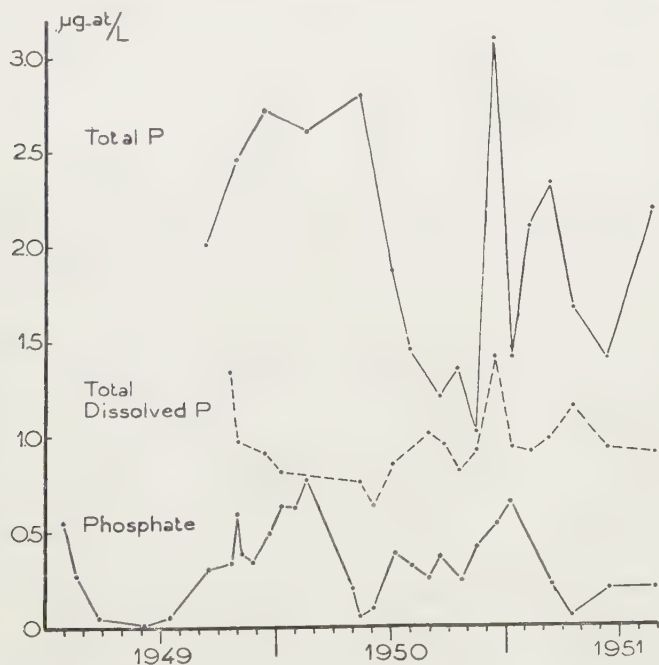


Fig. 48. Observations in the IJsselmeer near the sluices of Den Oever; phosphorus compounds.

phorus is a limiting factor for phytoplankton growth, since in spring phosphate is completely or nearly used up.

The data of stations 1-17 of fig. 13 may be used to form an idea of the quantitative distribution of phosphate. Some series of observations are given in fig. 46. The differences in phosphate-concentration from

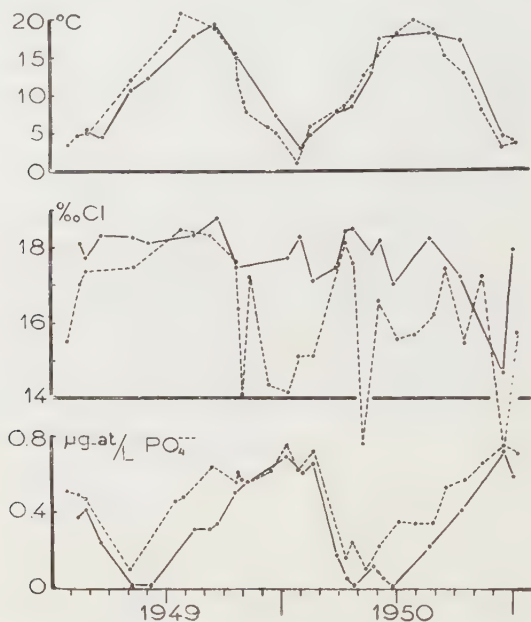


Fig. 49. Temperature, chlorinity and phosphate concentration of the North Sea (full-drawn line) compared with the Wadden Sea (dotted line). The North Sea values refer to observations about 15 km outside the Marsdiep; the Wadden Sea figures are averages of observations along the section of fig. 13; compare table 17.

station to station are small, although salinity differences are often considerable. Apparently, the phosphate-concentration of the IJsselmeer, contrary to what might be expected, is about as high as that of the Wadden Sea itself. This conclusion is borne out by measurements in the IJsselmeer, which show that the concentration is even somewhat lower there (fig. 47). — Further, phosphate in the North Sea will be expected to be about as high as in the Wadden Sea. Observations, however, carried out some fifteen kilometers outside the tidal inlet, show that PO₄-values are somewhat lower here too (fig. 49, table 17).

In view of the difference in phosphate content between the North Sea and the Wadden Sea and the exchange of water between the two areas, phosphate concentrations would be expected to increase slowly inward into the Wadden Sea. However, an examination of fig. 46 and all other data available shows that this is the

case in only a few sets of observations. In about as many cases the reverse is true and often there is no significant difference. Consequently, the fall from the standard of concentration of the Wadden Sea to that of the North Sea must take place in the relatively short stretch of about 15 km outside the tidal inlet. The following two reasons may probably account for this abrupt gradient. First, near the sluice of Den Oever the phosphate concentration is reduced in periods of a large supply of fresh water, because the IJsselmeer has a lower phosphate concentration than the Wadden Sea (fig. 47). Secondly, the fresh water discharged in relatively small amounts into the harbour of Den Helder contains very large amounts of phosphate, on an average about $20 \mu\text{g-at/l}$ (table 18). Therefore, the admixture of even small amounts of this kind of water already causes an appreciable rise of phosphate. In this way a phosphate gradient inside the tidal inlet is probably levelled out and the fall to the North Sea value must take place just outside the tidal inlet.

The fresh water discharged into the harbour of Den Helder originates from the Noordhollandsch Kanaal. The high phosphate content of the canal is partly caused by sewage from the town of Den Helder, partly supplied by a large area south of this town. That large quantities of phosphate may here be involved will appear from the following computation. The phosphate concentration being $20 \mu\text{g-at/l}$ and the water discharge per tide $0.8 \times 10^6 \text{ m}^3$, the quantity of phosphate supplied to the Wadden Sea amounts to $16.0 \times 10^9 \mu\text{g-at}$, or 480 kg per tide. For the IJsselmeer these figures are $0.3\text{--}0.4 \mu\text{g-at/l}$, $16.9 \times 10^6 \text{ m}^3$ per tide and $6.8 \times 10^9 \mu\text{g-at}$ phosphate or 204 kg of P per tide respectively. The canal therefore supplies more

TABLE 17

Phosphate and dissolved organic phosphorus in the North Sea; compare also fig. 47.

Date	Temp., °C.	Cl, ‰	PO ₄ , μg-at/l	Diss. org. P, μg-at/l	Total diss. P, μg-at/l	Station
1- 2-50	2.90	18.24	0.60	0.30	0.90	Outer buoy Molengat
1- 2-50	3.15	18.85	0.47	0.21	0.68	Lightvessel Texel
21- 2-50	5.03	17.12	0.60	0.23	0.89	Outer buoy Schulpengat
29- 3-50	7.56	17.43	0.17	0.46	0.63	Outer buoy Schulpengat
12- 4-50	7.88	18.37	0.05	0.63	0.68	Outer buoy Schulpengat
25- 4-50	8.51	18.44	trace	0.59	0.59	Outer buoy Schulpengat
25- 5-50	12.84	17.83	0.12	0.62	0.77	Outer buoy Schulpengat
7- 6-50	17.21	18.13	0.05	0.41	0.46	Outer buoy Schulpengat
27- 6-50	—	18.10	0.05	—	—	Lightvessel Texel
27- 6-50	—	17.04	—	0.58	0.58	Outer bouy Molengat
24- 8-50	18.11	18.18	0.22	0.56	0.78	Outer bouy Schulpengat
11-10-50	17.13	17.22	0.41	0.24	0.66	Outer buoy Schulpengat
20-12-50	4.47	14.64	0.72	—	—	Outer buoy Molengat, surface
20-12-50	4.42	16.68	0.50	0.17	0.67	Outer buoy Molengat, bottom
20-12-50	6.56	19.19	0.40	0.14	0.44	Lightvessel Texel, surface
20-12-50	6.71	19.16	0.36	0.14	0.50	Lightvessel Texel, bottom
3- 1-51	4.18	17.94	0.59	—	—	Outer buoy Schulpengat
6- 6-51	12.38	18.05	0.00	0.48	0.48	Lightvessel Texel
24- 8-51	18.00	17.27	0.18	0.65	0.83	Outer buoy Molengat
24- 8-51	18.01	17.82	0.21	0.54	0.75	Outer buoy Schulpengat

phosphate than the IJsselmeer. However, for total phosphorus the quantities are 650 and 1050 kg respectively, because the canal water contains only relatively little organic P, the IJsselmeer on the contrary considerable amounts (fig. 48).

Inside the harbour of Den Helder the large amounts of phosphate discharged with the fresh water cause an inverse relation of chlorinity and phosphate (fig. 50). Outside the harbour this relation soon becomes imperceptible.

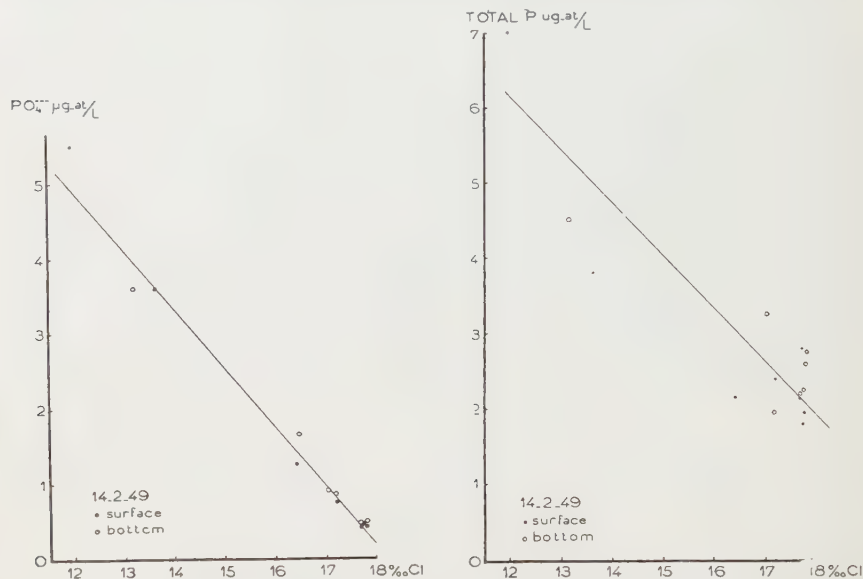


Fig. 50. Relation between phosphate, resp. total phosphorus, and chlorinity in the harbour of Den Helder.

Some sets of observations along traverses, running from Den Helder in a north-easterly direction, show that phosphate is evenly distributed through the whole Marsdiep area and adjoining areas (table 19). Higher values near Den Helder may again be explained from the influence of fresh water from the harbour.

B. Dissolved organic phosphorus

Measurements carried out along the section indicated in fig. 13 tend to show more pronounced differences in dissolved organic P from one station to another than in the case of phosphate (fig. 51).

In part these variations certainly represent actual differences, but they may to some extent, at any rate, also be due to less accurate analyses, although all determinations were run in duplicate; compare table 5.

Just as in the case of phosphate, the individual observations do not show a consecutive gradient of dissolved organic P in the direction of the North Sea or in the opposite direction. Nevertheless, as was shown

TABLE 18

Phosphorus content of fresh water discharged in the harbour of Den Helder; surface samples.

Date 1951	PO_4 , $\mu\text{g-at/l}$	Diss. org. P, $\mu\text{g-at/l}$	Part. P, $\mu\text{g-at/l}$	Total P, $\mu\text{g-at/l}$
14-2	18.6	5.1	0.4	24.3
4-4	8.8	4.2	1.6	14.6
21-6	24.3	6.1	0.7	31.1
4-8	21.5	7.2	4.1	32.8
13-10	20.3	9.1	1.4	30.8
15-12	26.1	1.6	3.3	30.9
average	19.9	5.5	1.9	27.4

TABLE 19

Phosphate concentrations along a traverse from Den Helder to Terschelling and back through the North Sea; 21 and 22 September 1949.

Time	Temp., °C.	Cl, ‰	PO_4^{---} , $\mu\text{g-at/l}$	
21 Sept.				
14.45	18.35	17.50	0.88	Marsdiep
15.00	18.44	18.28	0.65	
15.10	18.32	18.28	0.69	
15.30	18.09	18.33	0.56	Texelstroom-Omdraai-Oude Vlie
15.45	18.07	18.33	0.52	
16.00	17.73	18.33	0.42	
16.15	17.64	18.41	0.46	
16.30	17.83	18.41	0.41	
16.45	18.08	18.43	0.43	
17.00	18.19	18.48	0.50	Watershed Marsdiep-Vlie area
17.06	17.85	18.43	0.43	Inschot-Vlietstroom-Schuitengat
17.20	17.90	18.51	0.41	
17.35	17.73	18.49	0.41	
17.50	17.84	18.50	0.39	
18.05	17.84	18.44	0.45	
18.20	17.86	18.42	0.38	
18.35	17.82	18.43	0.36	
18.50	17.79	18.43	0.57	
22 Sept.				
6.30	17.40	18.43	0.50	
6.50	17.32	18.44	0.39	
7.05	17.64	18.46	0.41	
7.20	17.88	18.51	0.33	North Sea
7.35	18.09	18.51	0.31	
7.50	18.25	18.54	0.19	
8.05	18.29	18.51	0.35	
8.37	18.46	18.53	—	
9.07	18.52	18.65	0.26	
10.05	18.42	18.63	0.31	
10.35	18.40	18.34	0.32	
11.20	18.37	18.12	0.44	Marsdiep
11.35	18.29	18.12	0.44	
11.50	17.98	18.07	0.55	

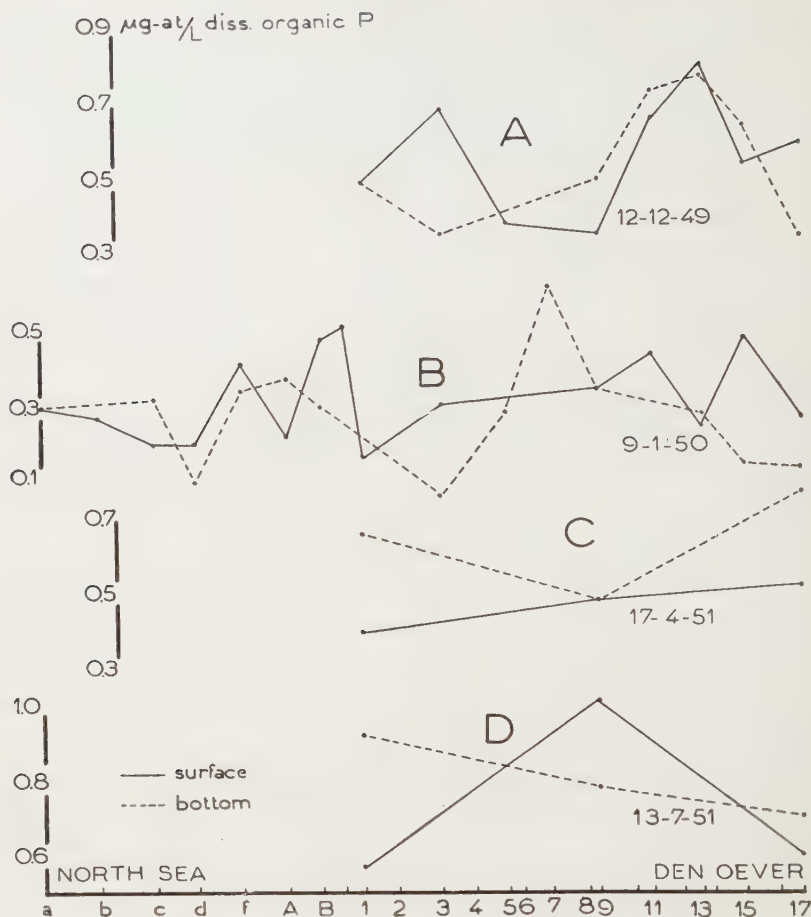


Fig. 51. Observations of dissolved organic phosphorus along the section of fig. 12.

by measurements carried out some 15 kilometres outside the tidal inlet, the concentration of dissolved organic P is lower in the North Sea than in the Wadden Sea (table 23, p. 505). Just as in the case of phosphate, the concentration of dissolved organic P in the IJsselmeer (see fig. 48) is not very different from that in the Wadden Sea, while the concentration in the fresh water discharged at Den Helder is higher (table 18). Thus the absence of a gradient of dissolved organic P may be explained in about the same way as in the case of phosphate.

The seasonal variation of dissolved organic P is roughly the reverse of that of phosphate, but runs parallel with that of particulate P (fig. 52). Apparently, the rise in organic suspended matter in spring on account of increased phytoplankton production is accompanied by a rise

in soluble decomposition products containing phosphorus. The maximum of approximately $0.8 \mu\text{g-at/l}$ is about as high as the winter value

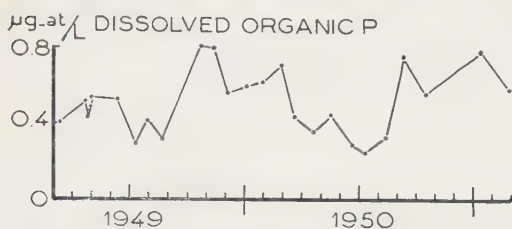


Fig. 52. Seasonal variation of dissolved organic phosphorus; averages of observations along the section of fig. 13.

for phosphate. In winter the concentration decreases to about $0.3 \mu\text{g-at/l}$. Thus complete mineralization of all dissolved organic P is never attained. Because the seasonal variation in phosphate content runs counter to that of dissolved organic phosphorus, the seasonal changes in total dissolved phosphorus

(phosphate plus dissolved organic P) are small (fig. 53). An inconspicuous minimum may occur in spring (1950: May-June, 1951: March).

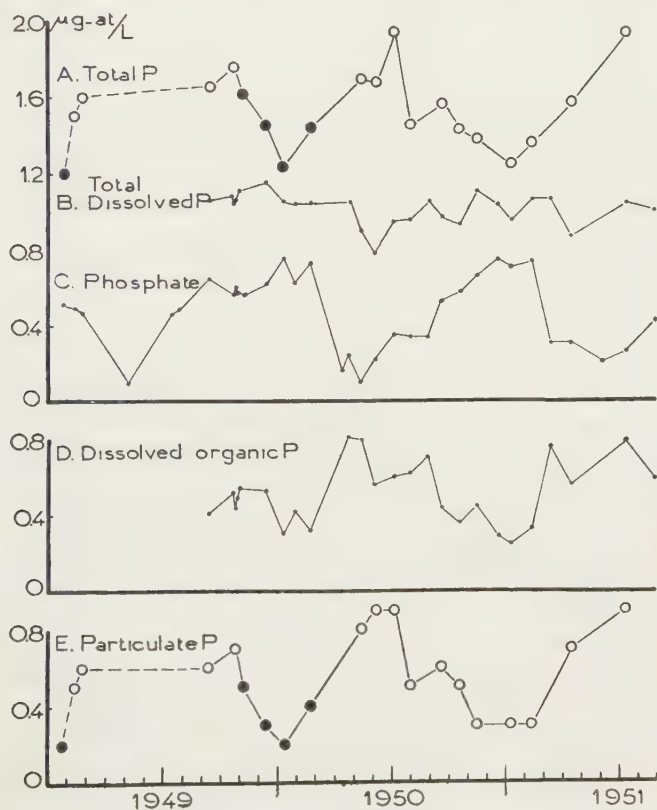


Fig. 53. Combination of figs. 43B, 44 and 52, to show the seasonal variation of total phosphorus and total dissolved phosphorus; for explanation see text.

C. Suspended organic phosphorus

As has been said before, suspended phosphorus may contain a small quantity of inorganically combined P, but it is believed to consist mainly of organic phosphorus. Since this component has been discussed already on p. 418, a single remark may suffice here.

Maximum concentrations of particulate P occur in spring and summer when conditions for phytoplankton growth are most favourable ($0.8 \mu\text{g-at/l}$, fig. 53); the concentration is at a minimum in winter ($0.2 \mu\text{g-at/l}$). Even in summer, however, only a small part of all the phosphorus present is actually contained in living matter: the particulate P itself will partly be present in detritus, while about one half of the total P will be present as dissolved organic phosphorus.

4. THE EXCHANGE OF PHOSPHORUS BETWEEN WADDEN SEA AND NORTH SEA

It has been shown in chapter III that the concentration of suspended matter is higher inside the Wadden Sea than outside. This gradient has been explained as resulting from the balance of two opposing influences. One influence, the exchange of water between Wadden Sea and North Sea, tends to level the gradient. The other, probably connected with the progressive decrease of current velocities from the tidal inlet to the coast, tends to accumulate suspended matter against the gradient. This accumulating mechanism only affects suspended material.

Not only suspended matter, however, but also its organic component (including particulate P) and also the dissolved P (phosphate and dissolved organic P) were found to be present in higher concentrations inside the Wadden Sea than outside. Though it must be admitted that the gradient of dissolved P, as compared with that of particulate P, is only small (no more than about $0.2\text{--}0.3 \mu\text{g-at/l}$ from the inner part of the Wadden Sea to the outer), even this small gradient must cause a net transport of dissolved P from the Wadden Sea to the North Sea.

Although the above value of $0.3 \mu\text{g-at/l}$ is only a very rough estimate, it will here be used in an attempt to calculate the loss of dissolved P to the North Sea. This will be done by means of the rate of the exchange of fresh water, which is 8%, as we found in chapter II. The result of a computation based on these data will give us some idea of the quantity involved in spite of the fact that the geographical distribution of dissolved P is different from the distribution of fresh water. As a matter of fact, the actual distribution of dissolved P even seems to point to a greater transport to the North Sea than the above 8%, because com-

paratively high concentrations of this substance are even found quite near the tidal inlet.

Since the high tide volume of the Marsdiep area is $3.1 \times 10^9 \text{ m}^3$, the total excess of dissolved P must be about $0.93 \times 10^{12} \mu\text{g-at/l}$ or 30,000 kg dissolved P. On the strength of the above percentage of 8%, we find that about 2400 kg of dissolved P would be transported to the North Sea in every tidal period.

The question may be asked how this loss is compensated. First of all it seems natural to suppose that dissolved P is brought into the area together with the fresh water. Water rich in phosphorus from the harbour of Den Helder, however, contributes only about 500 kg per tide (p. 487). The supply from the IJsselmeer cannot increase the amount of dissolved P in the Marsdiep area, as the concentration in the IJsselmeer is too low. The supply of dissolved P by the fresh water is therefore insufficient to cover the loss.

It might further be supposed that the loss is neutralized at the expense of the store of phosphorus in the bottom. There is indeed an extensive exchange of P between the bottom and the water overhead, but it seems improbable that this exchange should, on the whole, show a balance in favour of the water rather than the reverse. It is more reasonable to suppose that on an average the total amount of P in the bottom remains the same.

The improbability of a sufficiently large and continuous supply of P by the bottom to compensate for a continuous loss of about 1900 kg P per tide can be shown as follows. Determinations on a rather silty tidal flat near Den Helder enable us to make a rough calculation of the quantities of P present in the bottom. The total P content of 10 samples, from a traverse 250 meters in length, was found to vary between 10.8 and 4.9 $\mu\text{g-at/per gram of material}$ dried and free of salt – with an average of 7.3 $\mu\text{g-at/g}$ (table 20). Values of the same magnitude (about 10 $\mu\text{g-at/g}$) have been found by HÄNTZSCHEL (1939); compare also MOORE (1930, 1931). A bottom layer 1 cm in thickness may therefore contain about 73 mg-at or about 2 g P m^2 . The P-content of bottom animals, which is about 0.2 g P m^2 , can be left out of account¹. The Marsdiep area, covering $0.69 \times 10^9 \text{ m}^3$ (table 1), may thus contain about $1.4 \times 10^6 \text{ kg P}$ in a layer of 1 cm. Therefore, if the bottom should have to supply 1900 kg P per tide or about $1.4 \times 10^6 \text{ kg}$ per year, every year a layer of about 1 cm would be deprived completely of phosphorus. Such a process could not possibly continue over many years.

¹ VERWEY (1952) estimated the density of molluscs in this part of the Wadden Sea at some 10 individuals per m^2 ; a full-grown animal contains about 1 g of organic matter with a phosphorus content of about 1%. Hence these 10 animals contain about 0.1 g P. Other bottom animals may contribute the same amount.

TABLE 20

Phosphorus content of mud samples collected along a traverse over a tidal flat, Zuidwal, 11 September 1951.

<i>Nr.</i>	<i>Total P, μg-at/g dry material</i>	<i>Location</i>	<i>Nr.</i>	<i>Total P, μg-at/g dry material</i>	<i>Location</i>
1	10.8	Edge of bank	7	8.7	175 m
2	5.9	40 m from edge	8	7.6	190 m
3	4.9	70 m	9	6.6	205 m
4	5.8	100 m	10	7.8	220 m from edge
5	7.0	130 m			
6	8.2	160 m	average	7.3	

Since no sufficient quantities of P are supplied to the water of the Wadden Sea from the land-side or from the bottom of the Wadden Sea itself, it only remains possible to assume that the amount of dissolved P transported to the North Sea returns in some way or other from the same area.

In this connection the supposition developed in chapter III, that a balance of suspended matter is maintained between the North Sea and the Wadden Sea, might provide an explanation. As soon as the amount of particulate organic matter in the Wadden Sea decreases as a result of insufficient production, organic matter will be supplied from the North Sea, until a state of equilibrium is again attained. This means that the loss of dissolved P to the North Sea is neutralized by the transport of particulate organic P from the North Sea into the Wadden Sea.

The above assumption may also provide an explanation for the seasonal variation observed in total phosphorus (dissolved P + particulate P). Unless phosphorus is lost to other areas, the total phosphorus content of a certain mass of water will remain constant, whatever combinations may occur within the water mass itself. It appears from fig. 53 that in the Wadden Sea total P does not maintain a constant concentration all the year round, but is subject to seasonal changes. A minimum occurs in January and a maximum round about July. Apparently phosphorus is removed from the Wadden Sea water in autumn and supplied again in spring. We may ask how this is possible.

It might be suggested, that the seasonal variation in total phosphorus is caused by an exchange between the bottom and the water overhead, which would mean that phosphorus is released from the bottom in spring and taken up again in autumn. However, this is contrary to what might normally be expected. In spring and summer food is abundant and the bottom population increases and is more active,

thus causing the fixation of organic matter, including phosphorus, at the expense of the water overhead. The reverse may take place in autumn and winter.

On the other hand the exchange of phosphorus between Wadden Sea and North Sea might also account for the seasonal changes. In the author's opinion it is indeed this phenomenon which is the real cause of the changes in total P content in the course of the year. On the strength of the argument set forth in preceding sections we may assume that part of the suspended organic matter in the Wadden Sea is provided by the North Sea; a decrease of suspended organic matter in the North Sea would therefore also cause a decrease in the Wadden Sea. Since the quantity of suspended organic matter, hence also of particulate P, in the North Sea is higher in summer than in winter, the Wadden Sea will follow these variations. In this connection it is of importance to note that the variation in total P content is in the first place caused by variations in suspended P. The concentration of dissolved P in the Wadden Sea exhibits only minor changes (fig. 53). Attention may yet be given to the quantitative relation between particulate P, dissolved organic P and phosphate (table 23). In the Wadden Sea these substances are found in the ratio of 1:0.9:0.8 (average of all data available), which figures are more in favour of particulate P than those for the North Sea near the coast, where the ratio is 1:1.6:1.2 (average of data of table 17). To find an explanation for this difference we may pursue a line of argument analogous to the one followed before. In the Wadden Sea particulate P is constantly maintained in a relatively high concentration, which is always about 2-3 times as high as in the North Sea. Dissolved P, on the contrary, is exchanged freely and therefore never attains values considerably higher in one area than in the other.

The question finally arises, why also the concentration of dissolved P is higher, though only to a small extent, inside the Wadden Sea than outside.

In this connection it must be realized that the presence of large quantities of suspended matter within this area may in itself be a sufficient reason for the occurrence of a high concentration of decomposition products. If two separate water masses, one containing more particulate organic matter than the other, are compared under the same conditions and in a state of equilibrium, it may be expected that also the quantity of dissolved P in the first volume will be higher than in the second.

We should not unduly simplify matters by assuming that, if the Wadden Sea were to be separated from the North Sea, the former would (after some time) contain particulate P and dissolved P in the same ratio

as the North Sea. Still, if for a moment we allow this assumption, it may serve to illustrate the following point. The concentration figures of particulate P and dissolved P in the North Sea are $0.25 \mu\text{g-at/l}$ and $0.69 \mu\text{g-at/l}$ respectively (table 23). The Wadden Sea figure for particulate P is $0.5 \mu\text{g-at/l}$; on the above assumption dissolved P ought to have a concentration of $1.38 \mu\text{g-at/l}$. The difference between this theoretical figure and the concentration of $1.0 \mu\text{g-at/l}$ actually observed may be regarded as being due to the exchange of water between the two areas, which tends to reduce the value for dissolved P in the Wadden Sea to the North Sea concentration of $0.69 \mu\text{g-at/l}$.

No importance must be attached to the above value of $1.38 \mu\text{g-at/l}$. Nevertheless this hypothetical figure shows that an explanation of the higher concentration of dissolved P in the Wadden Sea simply as a result of the higher concentration of particulate organic matter is possible.

The amount of dissolved P may further be increased at the expense of particulate P through mineralization of the large amount of dead and living organic matter present on and in the bottom of the Wadden Sea. The quantity of organic matter that becomes decomposed will probably to a large extent be replaced by a supply of particulate P from the water overhead, although in some places bottom diatoms may also contribute to this amount (Grøntved, 1949). In this way the amount of dissolved P in the water may be increased at the expense of particulate P.

The part of the exchange due to the activity of molluscs allows of quantitative determination. The cockle (*Cardium edule* L.) and mussel (*Mytilus edulis* L.), which form the greater part of the animal bottom population, feed on suspended organic matter by filtering particulate material from the water. VERWEY (1952; see also LINKE, 1940) estimates that the quantities of suspended matter withdrawn in this way from the water by their combined filtering activities must be put at no less than $330 \times 10^6 \text{ kg}$ (dry weight) per year or $0.45 \times 10^6 \text{ kg}$ per tide; 11 % or 50,000 kg of this material per tide is considered by him as consisting of organic matter. However, his calculations refer to the whole area south of the watershed of Terschelling; if we consider only the Marsdiep area, this leaves $69,156 \times 50,000 = 22,000 \text{ kg}$ (compare table 1). This amount is partly used for the metabolism of the animals, partly converted into living tissue and for the rest rejected with the faeces. The metabolic products are directly returned to the water, the other products indirectly after having been stored in the bottom for a shorter or longer period.

The amount of particulate P strained from the water in this way is about 1 % of the organic matter, or 220 kg P, per tide. The greater

TABLE 21

The excretion of phosphate by the Cockle (*Cardium edule* L.) and the Mussel (*Mytilus edulis* L.).

Experiment I, 11-7-49. 18 Cockles, 4 l sea water t = 16.9°C Cl = 17.96 ⁰ / ₀₀			Experiment II, 26-6-50. 20 Cockles, 4 l sea water t = 17.1°C Cl = 17.18 ⁰ / ₀₀			Experiment III 20 Cockles, 4 l sea water t = 17.2°C Cl = 17.18 ⁰ / ₀₀		
Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per cockle, μg-at/l/h	Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per cockle, μg-at/l/h	Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per cockle, μg-at/l/h
0	0.78	—	0	0.87	—	0	0.70	—
6	0.96	0.49	30	1.36	0.20	30	1.05	0.14
20	1.54	0.55	60	1.95	0.24	60	1.40	0.14
35	1.93	0.35	90	1.95	0.00	90	1.50	0.04
50	2.35	0.37	120	1.95	0.00	120	1.55	0.02
80	2.60	0.11	150	2.40	0.18	150	1.80	0.10
145	2.80	0.04	180	2.90	0.20	180	2.25	0.18
Average		0.32	Average		0.14	Average		0.10

Experiment IV, 26-6-50 20 Cockles, 4 l sea water t = 17.1°C Cl = 17.17 ⁰ / ₀₀			Experiment V, 27-6-50 20 Cockles, 4 l sea water t = 17.1°C Cl = 17.19 ⁰ / ₀₀			Experiment VI, 27-6-50 20 Cockles, 4 l sea water t = 17.3°C Cl = 17.15 ⁰ / ₀₀		
Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per cockle, μg-at/l/h	Time, min.	PO ₄ , μg-at/l	PO ₄ -increase, μg-at/l/h	Time, min.	PO ₄ , μg-at/l	PO ₄ -increase, μg-at/l/h
0	0.63	—	0	1.11	—	0	0.58	—
30	1.05	0.17	30	1.53	0.17	30	0.99	0.16
60	1.30	0.10	60	1.46	0.00	60	1.20	0.08
90	1.32	0.01	90	1.82	0.14	90	1.38	0.07
120	1.40	0.03	120	2.40	0.23	120	1.69	0.12
150	1.70	0.12	150	2.40	0.00	150	1.82	0.05
180	1.90	0.08	180	2.80	0.16	180	1.60	—
Average		0.09	Average		0.12	Average		0.09

Experiment VI, 27-6-50
20 Cockles, 4 l sea water
t = 17.3°C Cl = 17.10⁰/₀₀

Experiment VII, 21-7-49
18 Mussels, 4 l sea water
t = 16.5°C Cl = 18.51⁰/₀₀

Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per cockle, μg-at/l/h	Time, min.	PO ₄ , μg-at/l	PO ₄ -increase per mussel, μg-at/l/h
0	0.78	—	0	0.55	—
30	1.16	0.15	15	0.80	0.10
60	1.35	0.08	45	1.02	0.09
90	1.47	0.05	105	1.45	0.09
120	1.88	0.16			
150	1.98	0.04			
180	1.80	—			
Average		0.09	Average		0.09

part of it will only return to the water after mineralization to dissolved P. In a state of equilibrium this amount will also be 220 kg P/tide.

Some laboratory experiments have shown that the cockle and mussel excrete considerable quantities of phosphate (table 21). About 20 cockles, collected on a tidal flat the morning or the day before the experiment, with an average size of about 3.5 cm, a wet weight without shells of 2 g and a dry weight of 400 mg, were for about three hours kept in a small aquarium containing 4 l of sea water of 17°C. The water, poor in phosphate, but containing a normal quantity of suspended organic matter, was kept circulating through the aquarium until the animals had opened their shells and could be expected to have started pumping; the supply of water was then cut off.

Apart from the exceptionally high phosphate production in experiment I, it was found that one cockle produced between 0.14 and 0.08 $\mu\text{g-at/l/hour}$, with an average of 0.103 $\mu\text{g-at/l/hour}$, or 0.037 mg/l $\text{PO}_4\text{-P/tide}$. This is equivalent to the decomposition of about 3.7 mg (dry weight) or organic matter per tide if the phosphorus content of the organic matter is assumed to be 1%. In this connection the experiments of MANN (1952), which indicate that cockles consume 180 mg of oxygen per kg (net weight) per hour are of interest. This figure is supported by observations on other molluscs (VAN DAM, 1935, 1938, HAZELHOFF, 1938; WHEDON and SOMMER, 1938; and KUENEN, 1942). It is equivalent to the decomposition of 4.1 mg (dry weight) of organic matter per tide per cockle of 2 g.

From the figures given by VERWEY (1952, p. 218–221) the number of cockles in the Marsdiep area can be computed at not less than 2.7×10^9 individuals. Assuming a consumption of 4 mg per cockle per tide, these animals appear to digest 11000 kg of organic matter/tide. It can also be calculated from VERWEY's figures, that these cockles retain on an average 18400 kg of suspended organic matter/tide if the organic percentage of suspended matter is supposed to be 11%. Since VERWEY's calculations are minimum estimations, this quantity may actually be twice as high and then amount to about 36000 kg/tide.

It follows from the above calculation that only part of the suspended organic matter passing through cockles and probably also mussels is mineralized within a short period. The residue is retained for a longer time in faeces, pseudofaeces and animal flesh and will be decomposed only gradually. However, the total amount of this material present cannot be estimated, the resistance of the faeces against decomposition under Wadden Sea conditions being unknown.

The figures given by VERWEY, which we used above, are minimum estimations, so that the actual amount of dissolved P returning from the bottom to the water may be larger than 220 kg/tide. Other animals will also make a contribution, so that in all perhaps 500 to 1000 kg P/tide is supplied to the water through the activity of bottom animals. The latter value is equivalent to 50,000–100,000 kg of organic matter, or 0.03 mg/l.

The value of 1000 kg dissolved P/tide constitutes about half of the quantity of 1900 kg dissolved P/tide, supposed to escape to the North Sea. The activity of bottom animals may therefore form an important contribution to the maintenance of the gradient of dissolved P from the Wadden Sea to the North Sea.

Besides through animal activity, dissolved P will be formed in the

bottom by bacterial decomposition of organic bottom material, originating from suspended matter which has settled to the bottom without being filtered by molluscs. The amount of this material is very difficult to estimate. Apart from this, it will be difficult to determine the rate of mineralization of this material.

Apart from high concentrations of organic matter, differences between Wadden Sea and North Sea of chemical and physical factors as salinity, temperature, and light penetration, might cause less favourable conditions for the growth of phytoplankton in the former area than in the latter, or a more rapid decomposition, and hence a higher concentration of dissolved P. Very little can be said about these possibilities, but it seems improbable that they will play an important rôle.

To sum up the points brought out in the foregoing discussion, we see that certain aspects of the phosphorus cycle find a natural explanation, if they are considered from a point of view that recognizes the close relation between suspended silt and particulate organic matter and takes into account the behaviour of suspended silt as described in chapter III.

The relations between North Sea and Wadden Sea appear to be rather complicated. There is probably a slow residual transport of organic matter from the former to the latter area during periods of rising concentrations of organic matter, while the reverse occurs when the concentrations of organic matter are falling. Of much greater quantitative importance, however, is the constant movement of organic matter from the North Sea to the Wadden Sea, which balances the transport of dissolved P in the opposite direction. The latter transport is caused by the fact that the concentration of dissolved phosphorus is higher in the Wadden Sea than in the North Sea.

The chief cause of the occurrence of this gradient of dissolved phosphorus is probably the activity of bottom animals, combined with the decomposition of large amounts of organic matter, accumulated both in the water and in the bottom of the Wadden Sea through the constant movement of suspended matter towards the interior. Chemical and physical differences between the Wadden Sea and the North Sea probably play only a minor rôle in this process.

Most important from a biological point of view is the conclusion that the production of organic matter within the Wadden Sea must be smaller than the rate of decomposition. The balance is restored by organic matter supplied by the North Sea.

5. THE PRODUCTION OF ORGANIC MATTER

From the previous discussion some insight has been gained into the quantitative difference between production and decomposition in the

Wadden Sea and its causes. However, this did not lead to a conclusion as regards the total quantities of organic matter produced or mineralized. An attempt will be made below to determine the approximate extent of organic production.

Because sessile plants are practically absent all organic matter originates from phytoplankton. To get an insight, therefore, into the productive capacity of the Wadden Sea, the quantity of phytoplankton present should, if possible, be determined. KREPS and VERJBINSKAJA (1933) and HARVEY (1934) introduced chlorophyll as a means of measuring this amount. The determination of chlorophyll has been discussed on p. 419.

In order to determine the amount of phytoplankton by means of chlorophyll it is of course necessary to know the chlorophyll percentage of phytoplankton.

Some confusion has been caused by the use of HARVEY's pigment units (HARVEY, 1934). One unit is equal to the green colour of 1 ml of a solution of 430 mg $\text{NiSO}_4 \cdot 6 \text{H}_2\text{O}$ and 25 mg $\text{K}_2\text{Cr}_2\text{O}_7$ in 1000 ml of distilled water. DEUBER (according to RILEY, 1938) and GUTHRIE (according to HARVEY, 1950) both compared this solution with pure chlorophyll. DEUBER computed that one pigment unit amounts to 0.88×10^3 mg of chlorophyll; GUTHRIE found 3×10^3 mg.

RILEY (1941), who probably used DEUBER's value, found on Georges Bank that 17.44 mg of chlorophyll (for the greater part contained in diatoms) corresponds with 600 mg of dry organic matter, including the ash; this works out a chlorophyll content of 2.91 %. However, the ash content of diatoms may amount to more than 40 % (BRANDT and RABEN, 1920); for ash-free organic matter the chlorophyll percentage may therefore rise to about 5 %.

PAGE (1941) found for cultures of *Nitzschia closterium* 2.32 %, also uncorrected for ash. He estimated the ash content at roughly 10 %, which means that for ash-free organic matter his percentage becomes only 2.59 %.

HARVEY (1950) determined the chlorophyll percentage in the sea off Plymouth indirectly by means of the relation between organic matter and phosphorus and between phosphorus and chlorophyll. One pigment unit was found to be equal to 0.0135–0.0175 mg of ash-free dry organic matter. If GUTHRIE's value were used, the chlorophyll percentage would amount to about 20 %, which is certainly too large. If DEUBER's value is used the chlorophyll percentage of ash-free organic matter decreases to 4.9–6.5 %. The value found by DEUBER is therefore certainly nearer the truth than the one given by GUTHRIE.

From determinations by GILLBRICHT (1951) in the Bay of Kiel it may further be concluded that the organic matter of diatoms contains 11.9 % chlorophyll and that of peridinians 4.0 %.

All things considered, a value of 6 % seems the best figure to use here as an approximation of the chlorophyll percentage of ash-free, dry phytoplankton.

Chlorophyll analyses in the Wadden Sea were started in April 1951; the observations are still continued. Complete data will be published in a separate paper, but table 22 and figs 54 and 55 may already give an idea of the average quantities and seasonal variations.

As can be seen from table 22, containing percentages found at the

stations 1, 9 and 17 between Den Helder and Den Oever (table 13), the chlorophyll concentration varies considerably from station to station with a decrease in the direction of the Wadden Sea interior. Nevertheless, the scarce data collected outside the tidal inlet indicate that the concentration of chlorophyll is considerably higher in the Wadden Sea than in the North Sea (fig. 55).

As appears from table 22 and fig. 54 the chlorophyll content of the Marsdiep area varies between about 30 mg/m³ in summer and 3 mg/m³ in winter, with an average of about 13 mg/m³. Assuming that all chlorophyll is contained in living phytoplankton and constitutes 6% of its organic part, about 0.5 mg/l of ash-free phytoplankton would be present in summer and 0.05 mg/l in winter, with an annual average of 0.2 mg/l.

TABLE 22

Chlorophyll concentrations in the Wadden Sea between Den Helder and Den Oever; stations 1, 9 and 17 of fig. 13.

Date	Depth ¹	Station 1		Station 2		Station 3	
		Chlorophyll mg/m ³	‰ Cl	Chlorophyll mg/m ³	‰ Cl	Chlorophyll mg/m ³	‰ Cl
13- 7-51	S	5	16.55	11	16.65	26	15.32
29- 8-51	S	(32)	12.48	15	15.84	14	15.65
5-11-51	S	15	16.03	14	14.38	(42)	1.79
12- 6-52	S	11	16.77	16	16.19	24	16.09
24- 7-52	S	20	17.14	17	16.54	6	16.51
	B	15	16.88	23	16.38	5	15.67
8- 9-52	S	22	17.68	10	16.91	12	15.41
	B	18	17.76	18	16.98	—	—
24-10-52	S	10	17.87	12	16.24	4	13.80
	B	6	17.87	13	16.62	7	14.39
12-12-52	S	4	14.31	5	14.78	7	11.93
19- 2-53	S	—	—	2	13.92	10	—
	B	12	13.15	—	—	2	15.27
24- 3-53	S	10	15.47	3	13.86	1	13.82
25- 3-53	S	11	16.27	12	14.22	2	14.08
	B	—	—	12	15.37	1	14.06
1- 5-53	S	19	17.43	—	—	8	14.16
	B	—	—	24	17.44	12	15.65
21- 5-53	S	5	17.73	7	17.32	3	16.84
	B	9	17.65	21	17.41	7	16.75
3- 7-53	S	20	16.86	21	15.97	7	14.86
	B	34	17.11	49	15.91	11	14.66
30- 7-53	S	15	16.13	23	15.75	11	14.28
	B	31	16.52	27	15.85	12	14.31
Average ²	S	15	—	13	—	7	—
	B	18	—	23	—	7	—

¹ S = surface sample, B = bottom sample.

² Data with surface samples only have been omitted.

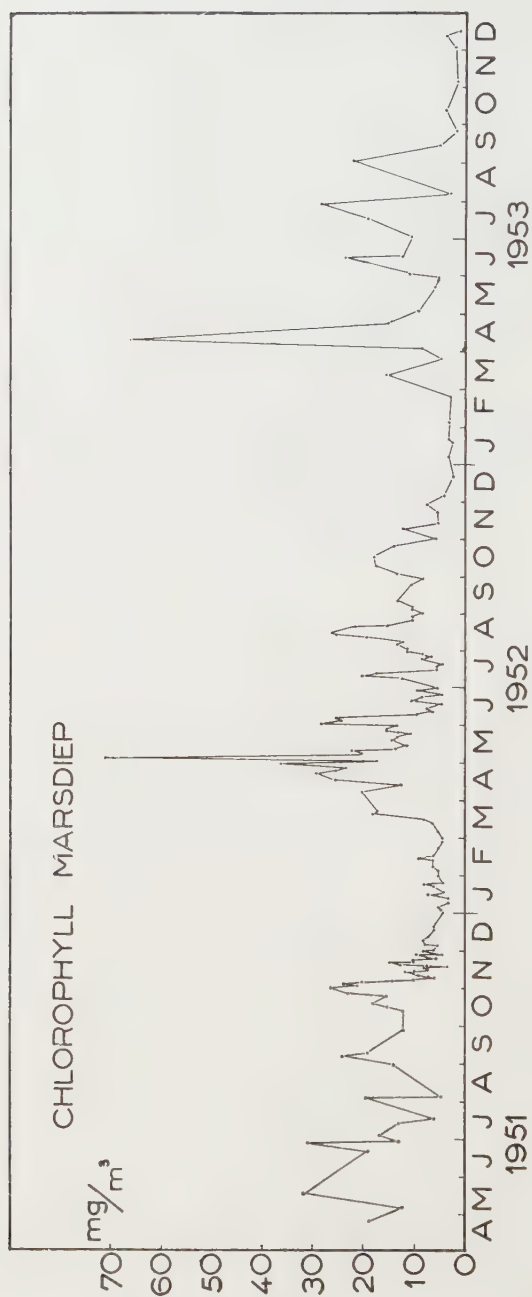


Fig. 54. Seasonal variation of chlorophyll; observations in the Marsdiep during high water.

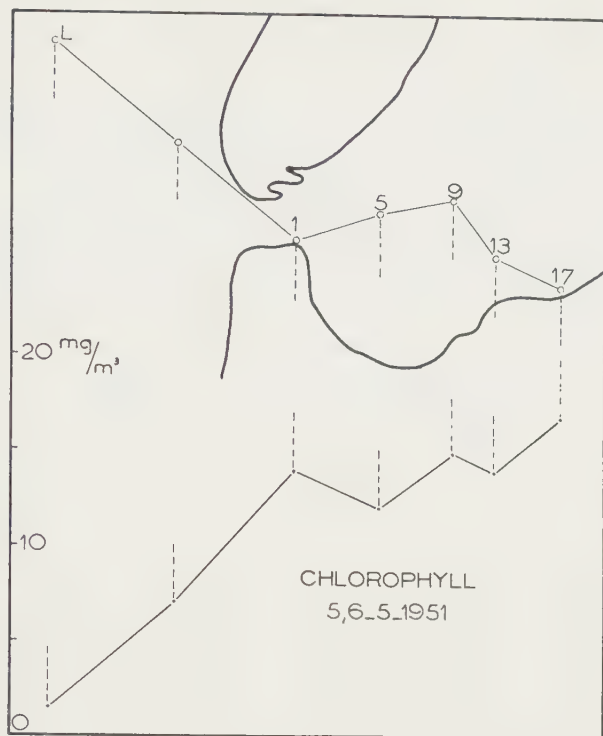


Fig. 55. Chlorophyll values of surface samples in a traverse through the Wadden Sea and into the North Sea.

However, part of the chlorophyll is probably not contained in living material, but incorporated in detritus. According to KREY (1951) and GILLBRICHT (1951) about 50 % of the chlorophyll in the Bay of Kiel may be contained in detritus. RILEY (1941) on the other hand puts this figure at 1 % for Georges Bank. If the percentage of 50 % is applied to the Wadden Sea, the average quantity of phytoplankton becomes only 0.1 mg/l; a value between 0.1 and 0.2 mg/l will be adopted for our further considerations. Since the average quantity of organic matter in the Wadden Sea is about 2.5 mg/l, only 4–8 % of all suspended organic matter in this area would then consist of phytoplankton. As the entire volume of the Marsdiep area at high tide is $3.1 \times 10^9 \text{ m}^3$, a total of about $0.3\text{--}0.6 \times 10^6 \text{ kg}$ of phytoplankton would then be present in this area. It goes without saying that this figure can be no more than a rough approximation.

Having approximately estimated the average amount of phytoplankton present, we may return to the question how much organic

matter may be produced in the Marsdiep area per unit time. Strictly speaking, a distinction should be made between "Gross production" and "Phytoplankton production", in which case the quantitative difference between the two would be constituted by the consumption of organic matter by the phytoplankton itself (RILEY, 1940). It is phytoplankton production that will be discussed here. To determine this production the rate of growth of the phytoplankton population must be known. LOHMANN (1908) observed in the Bay of Kiel an average daily growth of 30 %; also HARVEY (1950), from his own observations and those of others, assumes a daily production of 30 %.

This percentage will be applied to the Wadden Sea. It works out at a daily increase of phytoplankton of 0.03–0.06 mg/l (ash-free, dry weight), or 100,000–200,000 kg for the whole of the Marsdiep area. If we translate this into terms of phosphorus, on the assumption that organic matter contains 1 % P, the consumption of phosphate-P for the daily production would amount to 0.0003–0.0006 mg/l/day, or 0.01–0.02 $\mu\text{g-at/l/day}$ or 0.005–0.01 $\mu\text{g-at/l/tide}$, or 500–1000 kg P/tide, for the whole area.

Productivity estimates for other areas, comparable with the Wadden Sea, are scarce. Long Island Sound is probably a good example. RILEY (1941), from experiments with light and dark bottles, computes that the phytoplankton production there is 95–875 g of carbon/m²/year. The mean depth of the Sound being 20 m, this would be equal to 0.014–0.12 mg/l/day. To find the corresponding figures for organic matter from these carbon values, the latter must be multiplied by 2.3; this would give a production of 0.035–0.30 mg l/day, 3–15 times higher than the figure given above. However, conditions for phytoplankton growth are somewhat more favourable in the Sound than in the Wadden Sea. PRATT (1950), who carried out productivity experiments in concrete tanks, studied the relation between phosphate consumption and chlorophyll concentration; it can be derived from fig. 5 of his paper that phosphate is consumed at a rate of 0.07 $\mu\text{g-at/l/day}$ if the chlorophyll content is 10 mg/l. This means a production 3–7 times higher than the figure given above. Here, especially light conditions were more favourable in his tanks than in the Wadden Sea.

Although the figures found should of course be regarded with considerable reserve, we seem to be justified in concluding that the North Sea makes a significant contribution to the productivity of the Wadden Sea. For if our figures are approximately right the supply of organic matter from the North Sea (assumed to be about 2000 kg P/tide; see p. 493–494) would be of the same magnitude as the production of organic matter within the Wadden Sea itself (computed at 500–1000 kg P/tide).

SUMMARY

In this paper an attempt has been made to describe for the Dutch Wadden Sea water movement, transport of suspended matter and the cycle of suspended organic matter. Stress has been laid on the fact that these are related subjects, which therefore ought to be studied in combination. The discussion was based on observations made in the years 1949-1951 in the southwestern part of the area. A summary of the figures found from these observations is given in table 23.

TABLE 23

Comparison of average data for the North Sea, about 15 km outside the tidal inlet, with data for the Wadden Sea (Marsdiep area).

	<i>North Sea</i>	<i>Wadden Sea</i>
Chlorinity, ‰	18	16 (9-17)
Salinity, ‰	32	29 (16-31)
Suspended silt, mg/l	6	18
Suspended sand, mg/l	—	5
Total suspended matter, mg/l	—	23
Organic matter, summer, mg/l.	1.5	4
Organic matter, winter, mg/l	—	1
Organic matter, average, mg/l.	—	2.5
Phosphate, summer, $\mu\text{g-at/l}$	0.05-traces	0.10-traces
Phosphate, winter, $\mu\text{g-at/l}$	0.60	0.75
Phosphate, average, $\mu\text{g-at/l}$	0.31	0.49
Dissolved organic P, summer, $\mu\text{g-at/l}$	0.60	0.80
Dissolved organic P, winter, $\mu\text{g-at/l}$	0.20	0.30
Dissolved organic P, average, $\mu\text{g-at/l}$	0.38	0.53
Total dissolved P, average, $\mu\text{g-at/l}$	0.69	1.02
Particulate P, average, $\mu\text{g-at/l}$	0.25	0.60
Total P, average, $\mu\text{g-at/l}$	0.94	1.62
Chlorophyll, summer, mg/m^3	—	30
Chlorophyll, winter, mg/m^3	—	3
Chlorophyll, average, mg/m^3	—	13

For a good understanding of the results two facts appear to be of primary importance. First, there is a considerable exchange of water between Wadden Sea and North Sea, which is constantly at work to change Wadden Sea conditions, so that they approach those of the North Sea. Secondly, the concentration of light suspended material (silt) and of suspended organic matter is, notwithstanding this exchange, constantly higher in the Wadden Sea than in the North Sea.

1. *Water movement* (Chapter II).

In the southwestern Wadden Sea the vertical salinity gradient is only slight and the transport of fresh water is therefore mainly the result of

tidal mixing, while transport as a result of differences in density plays only a minor part. The mixing processes are greatly stimulated by differences in water movement between channels and tidal flats.

The rate of the exchange of water between Wadden Sea and North Sea resulting from these mixing processes was determined from the distribution of fresh water, which in its turn could be found from salinity figures. The average quantity of fresh water present in the area studied is 13 times the average amount discharged from the IJsselmeer during one tide. Therefore in every tidal period 8% of the total quantity of fresh water present within the Wadden Sea is transported to the North Sea. This percentage can be applied to every dissolved substance that has the same distribution as the fresh water.

A simple empirical method was developed to calculate the water exchange in a well-mixed estuary by means of a segmentation method. The figures calculated by means of this method for the amounts of fresh water present in the area studied were found to exhibit a significant correlation with those calculated from the salinity distribution.

2. *Suspended matter* (Chapter III)

Observations throughout a full tidal period at fixed stations and in distinct water masses marked by floats provided the basis for the study of suspended matter. The material was divided into two fractions, called "sand" and "silt", separated at a grain size of about $50\ \mu$.

The amount of material in suspension varies with current velocity. There is a time lag varying from a few minutes to one hour between the turn of the tide and the moment at which the minimum concentration of suspended matter is measured.

Large amounts of suspended matter are transported forth and back by the tidal streams; the total quantity of silt transported in every tidal phase through the Marsdiep amounts to 8×10^6 kg of dry weight. There is no conclusive evidence of a residual transport of silt in one direction or the other.

Although no substantial quantities of silt are supplied to the area by the IJsselmeer or by internal abrasion, the concentration of suspended silt is maintained at a higher level in the Wadden Sea than in the North Sea. The increase of the quantity of suspended silt inward is gradual and runs parallel with an increase in the silt content of the bottom.

The higher concentration of suspended silt in the Wadden Sea as compared with the North Sea is supposed to be caused by an accumulation mechanism resulting from a progressive decrease in water movement (especially a decrease in mean current velocity) from the outer to the inner part. The concentration actually observed is thought to

be the result of the balance maintained between this accumulation and the loss of silt through water exchange. The mechanism does not prevent the loss of dissolved substances.

3. *Organic matter.*

The cycle of organic matter was studied by determining the quantities of organic matter present, and computing the phosphorus content of water and organic material. The phosphorus is partly present as particulate P, partly as dissolved P. The particulate P is for the greater part contained in organic matter, while the dissolved P consists partly of organic P, partly of phosphate.

The quantities of organic matter, as well as those of the phosphorus components, are subject to annual variations. The largest quantities of organic matter and organic P (particulate as well as dissolved) are found in summer, whereas phosphate attains its maximum in winter.

The concentration of suspended organic matter (as well as suspended P) parallels the concentration of suspended silt and is therefore higher in the Wadden Sea than in the North Sea. It is supposed that the reason for this high concentration is the same as for the high concentration of suspended silt.

The concentration of dissolved P is also, though only slightly, higher in the Wadden Sea than in the North Sea. Since dissolved substances are exchanged freely, this causes a residual transport of dissolved P to the latter area. In every tidal period a net amount of 2400 kg of dissolved P is supposed to be transported to the North Sea. Fresh water from the harbour of Den Helder contributes to this quantity to the extent of about 500 mg/tide; the IJsselmeer, however, does not contribute to this amount, since the phosphorus concentration of the fresh water from this source is too low. The loss of the remaining 1900 kg of dissolved phosphorus is probably neutralized by the transport of the same amount of particulate organic phosphorus, incorporated in organic matter, from the North Sea to the Wadden Sea.

It follows from the foregoing paragraphs that part of the organic matter present in the Wadden Sea is formed in the North Sea. Another part will be synthesized by phytoplankton assimilation in the area itself. A rough estimate of this phytoplankton production has been made by means of chlorophyll determinations, which show that probably only 4–8% of the suspended organic matter consists of living phytoplankton. The highest phytoplankton concentrations occur in summer, the lowest in winter. The production of organic matter has been estimated from these data by assuming a daily growth of phytoplankton of 30% of its own weight. The production then appears to amount to 50,000–100,000 kg of organic matter per tide or 110 g m^{-2}

year. This quantity is equal to 500–1000 kg P/tide. The supply of organic matter by the North Sea, which would amount to some 2000 kg P/tide, would therefore be of the same magnitude as the production of organic matter within the southwestern Wadden Sea itself.

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COMPTES RENDUS DE LA SOCIÉTÉ NÉERLANDAISE DE ZOOLOGIE

JANVIER 1951 - DÉCEMBRE 1952

Séance du 13 janvier 1951 à Amsterdam

D. HILLE RIS LAMBERS (Bennekom). Biologie et écologie des Pucerons (Aphididae).

Un résumé de cette conférence n'a pas été remis au secrétaire.

Séance du 17 février 1951 à Leyde

1. C. L. DEELDER (Heemstede). A contribution to the knowledge of the stunted growth of Perch (*Perca fluviatilis* L.) in Holland.

Voir: Hydrobiologia, **3**, pt. 4, 357-378, 1951.

2. A. F. J. PORTIELJE (Bennebroek). Symbolic expression of the sexual instinct (urge to coition) in a male One-wattled Cassowary (*Casuarius uniappendiculatus* Blyth.) and experiments with removed eggs and nests of the Herring-gull (*Larus a. argentatus* Pontopp.). Illustrated with documentary films.

An initial abstract was given on the structure of an instinct and of the relations in a whether or not complete instinctive behaviour. Then a short survey was given on instinctive symbolic expressions in animals, moulded into form and expression by the unconscious biological psyche (at least at the outset) being in force as an organisatrix, constantly bringing about an actual psychical or "total" ordering of physiologically given order, and restoring in this way the labile natural equilibrium, the broken harmony between internal factors mutually and with respects to external ones.

Instincts are thinkable as fundamental psycho-physical potencies, integrative primordial factors or indispensable momenta (yet not atomistic "elements"!) of the biological psyche, the whole of "many-in-one" organised functions of a psycho-somatic individual, acting and reacting as a totality" (PORTIELJE, 1948).

In the periodically coming to the service of instincts (the once

ripened bodily abilities as "historized" neural patterns being in a life-long readiness for actual use) "symbolic expression of instinctive forces drags them out into the open, differentiates them and delineates them" (WHITEHEAD), moreover it is used in an unconsciously regulated way to vent a more or less "dammed up" drive. This in case the individual is not (yet) able to realise its instinctive potencies in a completely fulfilled cognitive-affective-conative striving, either because the drive is still in an insufficiently developed state; or in case a drive, which is already fully developed subjectively and moreover intensely welling up in the individual, is "blocked" objectively, as the "adequate" or rather accessory constellation in the environment (marked by a specific configuration of sense-stimuli, perceived and appreciated by the animal in question and seeming to have a certain "meaning" or "value" for the striving individual) is wanting or not at all apt for co-operation. Contrary to both forms of symbolic expression mentioned above, another more or less explosive form may be observed, which, showing similarity as well as polarity with the former ones, must be distinguished, not separated, however, from them. In both the former ones a rather poorly rising appetite effects the gradually welling up of a drive which – being checked subjectively as well as objectively because of either unripe or still insufficiently developed innate abilities, together with a not attainable, respectively unresponsive, goal – is slightly dammed up and vented in a whether or not objectless symbolization.

In the latter, on the contrary, a strong appetite effects an intense, somewhat explosive drive, executed by means of fully ripe and well-developed abilities, which – being blocked by objective circumstances – is highly dammed up and vented in a more or less impetuously expressed symbolization of function and object, respectively situation, in the transferring upon which an abrupt lowering of the "threshold-value" in the cognitive-affective-conative striving is evolved (PORTIELJE, 1948).

The Cassowary produced an instinctive symbolization of function and object by means of transferring, in which the natural "seeking" and "choosing" (as the essential central phenomenon in purposive behaviour) subjectively aroused, was objectivated and directed upon a shovel as a representative "symbol" for the natural object, the hen.

The experiments with removed eggs and nests of the Herring-gull made clear, that the breeding partners got into a psychical or total conflict, in which an ambivalent behaviour was produced, directed either to the removed nest or to the original situation, in which it was build. The actions-and-reactions came to an end in a nesting and breeding between the removed nest, from which the eggs and nesting material were taken, and the original nesting-situation.

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PORTIELJE, A. F. J., Premarital behaviour in the Condor (*Sarcoramphus gryphus* L.). Bijdr. Dierk., **28**, 359-371, 1949.

Séance du 17 mars 1951 à Amsterdam

1. L. D. BRONGERSMA (Leyde). On the arteria pulmonalis in the Boidae and in some other snakes.

In the majority of the Boidae two well developed lungs are present; this is also the case in *Xenopeltis unicolor* Reinw. In the Anilidae, the genus *Cylindrophis* has a very small, but still well developed left lung, while the left lung is rudimentary in *Anilius scytale* (L.). In these snakes the pulmonary artery originates from the ventricle as a single stem, which divides into the ramus dexter and the ramus sinister. While in all other amniotes the ramifications of the ramus dexter are confined to the right lung, this is not the case in snakes with two well developed lungs. In these the ramus dexter sends ramifications to the left lung. In many species the systems of the ramus dexter and ramus sinister are connected by anastomoses. Thus, in *Python reticulatus* (Schn.) a direct anastomosis is present between the ramus dexter and the ramus sinister; moreover, the smaller ramifications of these rami are also connected and an arterial network is formed around both lungs. In the Boid *Calabaria reinhardtii* (Schl.) the ramus sinister has disappeared: a branch of the ramus dexter is the sole vessel that supplies the left lung with blood. In the Boidae *Tropidophis* and *Trachyboa* the left lung has disappeared, but a tracheal lung has developed; the ramus dexter divides into two branches, one anterior to the tracheal lung, and one posterior to the right lung.

2. N. POSTMA (Utrecht). Les effets de la deuxième et de la troisième ligature de STANNIUS chez le cœur de Grenouille sont-ils soumis à une seule condition?

La deuxième ligature de STANNIUS appliquée au sillon auriculo-ventriculaire cause la reprise des battements périodiques du ventricule. GOLTZ l'attribuait à l'excitation mécanique continue exercée par cette ligature sur le sillon ou sur le ganglion de BIDDER, situé au même niveau (1861).

Nous avons trouvé récemment qu'à côté de l'excitation mécanique continue, ou même au lieu de celle-ci, l'abaissement du seuil de l'excitation (ou de l'automatisme) pourrait être la cause de l'effet mentionné. Des ligatures précédentes ayant enfermé du sang dans les oreillettes et le ventricule (première ligature) ou seulement dans celui-ci (deuxième ligature), la pression exercée sur ce sang par la ligature distend la

paroi cardiaque, ce qui augmente l'excitabilité. Les phénomènes provoqués au ventricule, respectivement à la base ($\frac{2}{3}$) du ventricule, par la deuxième et la troisième ligature, savoir: le fonctionnement de l'automatisme ventriculaire, respectivement l'accélération de la fréquence à la base du ventricule, peuvent donc être réduits à un seul dénominateur.

De même HAYWOOD et MOON (1950) rendent la distension alternante des bouts du tube responsable du fait que l'inversion de la direction des ondes de contraction dans le cœur tubulaire des Tuniciers, se manifeste plus souvent selon que l'activité cardiaque augmente. Au contraire l'inversion devient rare aussitôt que le cœur est isolé de l'animal et dépourvu par là des systèmes capillaires adjacents, causant en raison de leur résistance la distension du tube cardiaque par accumulation du sang. Malheureusement ces auteurs n'ont pas exposé le cœur résectionné à des résistances artificielles pour démontrer expérimentalement la validité de leur conception.

(Les expériences seront publiés ailleurs plus en détail)

Séance du 19 mai 1951 à Utrecht

I. H. A. L. TRAMPUSCH (Amsterdam). Inhibition and stimulation of regeneration.

A. The gradient of the regenerative capacity along the stem of *Tubularia*.

Literature contains various data which justify the supposition that the regenerative capacity of Hydroids, after these have been severed at different levels, shows great diversity. As the animals observed were of somewhat labile forms, i.e., *Hydra*, similar experiments were made on *Tubularia* where the form is far more constant by reason of the substantial perisarc. Since comparison is, however, only possible with pieces of equal length, the fragments required for the experiment had to be cut to measure at both ends. In order to prevent the two surfaces exercising a disturbing influence on one another, the regeneration of one end of the stem pieces was prevented by constriction with a nylon thread or by coagulation through a specially constructed high-frequency micro-cautery, thus rendering the fragments unipolar. The results of both methods were closely identical and could ultimately be summarised under a single heading.

Series of stem pieces, 8 mm in length, and cut off at 1 mm, 3 mm, or 5 mm beneath their "neck" (the constriction of the animal immediately under the hydranth) were, after being made unipolar, given the opportunity to regenerate at a temperature of 22° C. The progress of regeneration was observed every two hours, and the time required by each animal in reaching one of four previously determined stages, was

registered. After calculation of the averages, it proved that the stages 1 and 2, i.e., "striated" and "pinched" were much more swiftly attained in pieces beginning at 1 mm beneath the neck, (tail-error less than 1 %) than was the case with those severed at 3 or 5 mm. The significance of these differences for the achievement of the later stages of regeneration is less pronounced. The proximity to the neck at which equal lengths of *Tubularia* are cut off, therefore, influences the speed of regeneration.

B. The relation between regenerative capacity and metabolism.

As it is possible to relate a gradient of regenerative power to metabolic processes, the influence was examined of chemical substances known to check or stimulate metabolism, on regeneration. For this purpose ranges of temperature were used corresponding to the lowest and highest point in the habitat of the animals, viz. 17° for the former and 23° for the latter. Here also pieces from various stem levels were employed and compared with controls cultivated in pure seawater. The experiments showed that some substances, as for instance, Lithium-chloride, retard regeneration at low, and stimulate it considerably in the same concentration, but at higher temperature. Methylenblue soluted in a percentage of $5.10^{-4}\%$ stimulates at 17° but delays regeneration in a concentration of $10^{-3}\%$ at a higher temperature. Pyrocyanide in a concentration of $3.10^{-4}\%$ has a significant slowing-up influence, while the effect of weak solutions is dubious.

Stress is laid on the importance of collecting data dealing with the activity-range covered by various substances governing regeneration through metabolism. If we had knowledge of these values it would presumably become possible to command the processus of regeneration. At the same time generation – in so many respects similar to regeneration – may become intelligible to us.

2. D. STEGWEE (Amsterdam). L'action du parathion et du D.D.T. sur le cholinestérase chez la Blatte (*Periplaneta americana* L.).

Voir: Biochim. biophys. Acta, **8**, 1952, 187-193.

3. J. HOFKER (La Haye). The forming of species of Foraminifera during the Upper Cretaceous.

Study of many cores of drillings through the Upper Cretaceous of Holland and Germany enabled me to analyse the development of many species of Foraminifera during the Upper Cretaceous, which is characterised by the raise of so many groups of Foraminifera. Several different modes of altering of species into new ones were observed. In the genera around *Gavelinella* (*Gavelinella*, *Gavelinopsis*, *Stensiöina*, etc.) many species begin their course through time with very fine pores in the test walls, which pores gradually increase in size up to a diameter of about 8μ . Then each species extends; when the diameter of the pores reaches

about $4\ \mu$, suddenly the species may give rise to varieties which continue to enlarge their pores but differ from the original species in some characteristics (I), or a totally new species or several new species with quite different characters may be formed which once again begin their course with very fine pores (II). A second form of altering into new species is, contrary to this sudden alteration, gradually, since then a special character alters gradually during a long period of time into the end-form of the species, which endform differs so greatly from the original form, that one would be inclined to give it a quite different specific name(III). This phenomenon was found in many species of the Lagenidae, viz. *Neoflabellina* and *Fronicularia*, and has been described also by BETTENSTAEDT in the genus *Globorotalites*; I found it also in *Gyroidinoides*. There exists a fourth modus of alteration also, which seems to be connected with alteration in the modus of reproduction; in those forms at the beginning of the evolution of a species the species is trimorphic (statistically stated), whereas in the course of time the species becomes dimorphic or even apogamic. In the latter case, when the generations are different in shape or characters, the characters of one of the generations are the remaining ones in the end of the development, mostly those of the microspheric form (IV). In some groups, viz. *Bolivinooides*, it was stated that in dimorphic species the younger species in its microspheric form shows the characteristics of the older species from which it obviously derived, whereas the new species in its megalospheric tests shows the characteristics of the new species.

In the case I the new varieties, continuing the course of evolution of the original species, seem to be real varieties, not those found horizontally (in the same geological period) around the main form, but vertically; the enlargement of the pores is obviously a character which is a function of time (anciennity) of the species.

In case II there seems to be question of real mutation into a new species, which once again begins as a young one and gradually becomes older.

In case III there is quite a difference with case I; for in I it was stated that the development of a new variety was discontinuously, whereas in III the alteration is gradually; so here special characteristics show the function of time, such as the gradual enlargement of the size of the pores. These alterations may be called gliding "varieties", but there are no real borders between a species and the younger form into which it develops. It is a typical fact that all those alterations are not limited to a certain geographic place but that they are found all over the world in a special period. The same can be said about case IV; this form of alteration was found in many groups, but especially in planktonic or pelagic groups, such as *Globigerina* and *Gümbelina*. So it

may be an adaptation to pelagic life, but is also a function of time. Moreover, it was stated that at the end of the development of a whole group of closely allied species, forms occur which show characteristics of the species which are found at the beginning of the development (*Globotruncana*, *Gümbelina*, *Bolivina*, *Bolivinoïdes*, etc.).

This fact, also known among other groups of animals (Ammonites), points out that the taxonomy of Foraminifera has to be studied along the same lines as in other metazooid animals. Moreover, it could be stated that when using finer methods of analysing Foraminifera, long-living species are very rare and that most species do not live longer than some ten millions of years.

Séance du 10 novembre 1951 à Leyde

1. F. SOBELS (Utrecht). Quelques aspects d'un analyse génétique et morphologique du mutant "Asymmetric" de *Drosophila melanogaster*.

Voir: Trans. IX Int. Congr. Entomol., **1**, 225-231, 1952. *Genetica*, **26**, 117-279, 1952.

2. K. VAN ASPEREN (Utrecht). Le métabolisme du méthylthiouracile chez le Coq.

Voir: Tijdschr. Diergeneesk., **76**, 133-155, 1951. *Biochim. biophys. Acta*, **8**, 150-161, 1952.

3. P. F. VAN HEERDT. La variabilité de la longueur du forceps chez le mâle de la forficule (*Forficula auriculata* L.).

Voir: Ent. Ber., Amst., **14**, no. 341, 383, 1953.

Séance du 15 décembre 1951 à Amsterdam

1. L. BELS (Rotterdam). Fifteen years of Bat-banding in the Netherlands.

Voir: Publ. Natuurh. Genoot. Limburg, no. 5, 1952.

2. J. W. SLUITER (Utrecht). Le cycle reproductif des Chiroptères.

Voir: Vakbl. Biol., **32**, no. 6, 107-115, 1952.

Séance du 2 février 1952 à Amsterdam

A. PUNT (Utrecht). Le cœur artificiel.

Un résumé de cette conférence, qui fut illustré avec un film démonstratif, n'a pas été remis au secrétaire.

Séance du 15 mars 1952 à Utrecht

1. J. VERWEY (den Helder). La propagation des moules (*Mytilus edulis* L.) et des coques (*Cardium edule* L.) sur les sables du "Waddenzee". Un résumé de cette conférence n'a pas été remis au secrétaire. M. le docteur VERWEY a donné un résumé des travaux concernant ces sujets, exécutés au station zoologique de la société néerlandaise de

zoologie à den Helder. Aussi il a précisé les recherches futures. Les résultats seront publiés dans: Arch. néerl. Zool., **11**.

2. J. VAN DER VECHT (Bogor). Observations sur *Rodopholus oryzae* (v. Breda de Haan) Thorne, nématode parasite du riz en Indonésie.

Voir: Contr. gen. agric. Res. Sta. Bogor, 1952.

Séance du 26 avril 1952 à Leyde

1. J. DE WILDE (Amsterdam). Aspects of diapause in adult insects (with special regard to the Colorado Beetle, *Leptinotarsa decemlineata* Say.).

Voir: Arch. néerl. Zool., **10**, no. 4, 1954.

2. M. ROOSEBOOM (Leyde). The influence of the invention of the microscope on biological Thinking.

Whereas the telescope was, as soon as it was invented (c. 1609), applied systematically in scientific astronomy, the microscope remained for some decades a curiosity rather than a scientific instrument.

Several reasons can be given for this slow development of scientific microscopy. First of all, the microscope was in the beginning a poor instrument. Secondly, the scientists, biassed by mediaeval ideas, were so utterly unprepared to find a microscopic living world, that no scientific problems were awaiting their solution by this instrument as was the case with the telescope.

Small insects known from daily life (fleas, mites, etc.) were the first objects to be observed. Admiring amazement at the minute and perfect structures in these despicable creatures predominates in the descriptions of the first half of the 17th century.

The discovery of a multitude of macroscopically invisible organisms dethrones the mites in meal and cheese as "living atoms" and leads into speculations on the infinite smallness of living structures in microscopic organisms: the "incomparable stenography of Providence".

MALPIGHI, finding human microscopical anatomy too difficult to understand, shifts first to the silkworm and then to plant anatomy, hoping to find simpler parallels providing the key to the explanation of human functions. When these investigations fail to lead to the expected results, he is only prevented from proceeding to the study of crystals by the weakness of his health.

The doubt whether the lower creatures are built on the same plan as the higher organisms is one of the important results of microscopy.

Séance du 24 mai 1952 à Amsterdam

P. KORRINGA (Bergen op Zoom). Investigations on shell-disease in the Oyster, *Ostrea edulis* L.

Voir: Rapp. Proc. Verb. Cons. Int. Expl. Mer, **128**, no. 2, 50-54, 1951.

Séance du 19 septembre à den Helder

1. H. POSTMA (den Helder). Observations concernant l'échange d'eau entre le mer du Nord et le "Waddenzee".

2. I. KRISTENSEN (den Helder). Propagation et croissance du coque (*Cardium edule* L.).

3. J. DE BLOK (den Helder). L'établissement premier des larves de moule (*Mytilus edulis* L.).

4. P. M. L. TAMMES (Wageningen). Le renouvellement de l'eau respiratoire des moules et l'influence de la grandeur et de la concentration des particules suspendues sur la filtration des branchies.

5. H. GEELLEN (Utrecht). La préférence des Nudibranches pour certains Coelentérés.

6. J. WESTENBERG (den Helder). La question de la pêche excessive.

Ces conférences, dont les résumés n'ont pas été remis au secrétaire, donnent une idée des travaux exécutés au Station zoologique à den Helder. Les recherches seront publiées dans le périodique Archives Néerlandaises de Zoologie.

Pour la conférence de P. M. L. TAMMES voyez: Arch. néerl. Zool., **10**, 153-160, 1952.

Pour la conférence de Mlle H. GEELLEN voyez: Arch. néerl. Zool., **10**, 161-170, 1952, et aussi Arch. néerl. Zool., **10**, 241-264, 1952.

Pour la conférence de J. WESTENBERG voyez: Arch. néerl. Zool., **10**, 290-314, 1952.

Séance du 1 novembre 1952 à Utrecht

J. VAN IERSEL (Leyde). On the orientation of *Bembex rostrata* L.

The subject has been partially discussed in the following publication: Trans. IX Int. Congr. Entomol., **1**, 384-393, 1952.

Séance du 20 décembre 1952 à Leyde

I. A. G. VLASBLOM (Leyde). The function of the "mast" on the nest of *Hydrous piceus* L.

The idea that the "mast" of the nest of *Hydrous* serves in some way or the other as a means of providing the eggs and larvae with oxygen has been put to the test by WESENBERG-LUND, who stated that the eggs developed only when at least the tip of this funnel projected above the surface of the water.

LAABS, however, experimenting with the nest of another species, *Hydrophilus caraboides* L., found that eggs in nests of which the funnel was removed and which were covered with a coating of lacquer, developed normally. Accordingly he rejects WESENBERG-LUND's suggestion.

The results of the experiments of WESENBERG-LUND could, however, be confirmed, whilst micro-analysis of the gasmixture in the nest showed that, in totally immersed nests the oxygen concentration sank

to values as low as 4%. In those cases where the tip of the funnel projected into the air the oxygen percentage amounts to 14%. In nests floating on the surface, eggs develop normally even when the funnel has been rescinded or throttled by a thread noose.

The foregoing facts substantiate WESENBERG-LUND's supposition that the funnel serves as a safety device acting in those cases where the bulk of the nest becomes submerged.

2. K. H. VOOUS (Amsterdam). The aims and the results of an ornithological survey of the Netherlands Antilles.

On behalf of the "Netherlands Foundation for the Scientific Research of Surinam and the Netherlands Antilles" speaker and his wife spent about 8 months in the Netherlands Antilles (1951-1952), collecting specimens, gathering field observations on habitat, behaviour, breeding season, migration, etc., and comparing the bird life on the various islands visited. Problems on bird migration have also been studied. Speaker demonstrated study-skins of some of the interesting or noteworthy species collected and showed a number of colour-slides of the breeding colony of flamingoes (*Phoenicopterus r. rubes* L.) on Bonaire and of the bird life (mainly terns and a species of gull) on the little known island of Klein-Curaçao.

3. H. L. DE FLUITER (Wageningen). Insects as vectors of plantviruses. The strawberry aphid (*Pentatrichopus fragaefolii* Cckll.) as a vector of strawberry viruses.

HARRIS, KING, PRENTICE, *et al.*, made a thorough study of the strawberry viruses in the British Isles; they concluded to the presence of at least 3 viruses, *viz.* virus 1 (mild crinkle), virus 2 (mild yellow edge) and virus 3 (severe crinkle). These viruses are considered to be distinct since they differ in vector relationships (minimum infection feeding period required for transmission = acquisition threshold; inoculation threshold, persistence in the vector), in the incubation period of the diseases they cause and in the symptoms produced on the indicator plant, the wild strawberry, *Fragaria vesca*. In the field the viruses often occur in combination, resulting in the production of much more severe symptoms. The aim of the authors work is to investigate which viruses are present in Holland and how they can be controlled. The technique used to isolate the different viruses is based on the vector relationships of the viruses (see PRENTICE).

The natural mode of spread of the viruses is by the agency of the strawberry aphid, *Pentatrichopus fragaefolii* Cckll., which appeared to be the most important vector in this country. The aphid is very common in our strawberry fields where it feeds preferably on the young leaves, the petioles and the runners. It is a small pale green aphid provided with a lot of knobbed hairs.

Experimentally virus transmission also can be obtained by grafting and by dodder (*Cuscuta* div. spec.). In recent time mechanical transmission by means of rather complex chemical methods also leads to some results. Seedlings are always free from virus.

The object of the "General Netherlands Inspection Service" for seeds of field crops and for seed potatoes (N.A.K.) is to further the production and use of reliable propagating material of field crops as well as the improvement of such material.

The points it endeavours are, *e.g.*, a. encouraging the improvement of varieties of field crops (among which strawberries) and their growing free from diseases; b. promoting the use of certified Dutch propagation material at home and abroad; c. encouraging research in relation to inspection methods.

These points underly our investigations on the strawberry viruses and their vector in our country. Concerning these investigations the following remarks can be made. In the laboratory we breed virus free strawberry aphids and allow them to feed for a predetermined time (infection feeding period) on suspected plants (the infector), collected in the fields and taken into the laboratory. Then the aphids are transferred to a series of wild strawberry plants (*Fragaria vesca*, East Malling clone or seedlings of *Fragaria vesca*) which are used as indicator plants. After the appropriate period (first transfer feeding period), the aphids are transferred to a fresh set of indicators for the second feeding period and subsequently retransferred to other series of indicator plants.

By means of the minimum infection feeding period required for transmission of the virus, the persistence of the virus in the vector, the period needed for development of the first symptoms on the indicator plants and the symptoms produced, we try to separate and to identify the viruses. The virus investigations have to run hand in hand with investigations on the biology, the epidemiology, and the behaviour of the vector, the strawberry aphid. The most important facts studied and mentioned are:

the life cycle of the aphid in Holland;
the time of occurrence of the winged specimens;
the factors which influence the increase and the decrease of the population density in the course of the year;
the wild host plants, and
the control of the aphid.

The results of these investigations were briefly mentioned; they will be published in extenso elsewhere.

References: Ann. Appl. Biol., **33**, 1946; **35**, 1948; **38**, 1951. J. Pomol., **19**, 1942; **22**, 1946.

ERRATA

Mr J. H. Stock of the Amsterdam Zoological Museum kindly drew my attention to some errors crept into the section 'Pycnogonida' of my paper in this volume 'The shell of *Ostrea edulis* as a habitat' (p. 32-152). After having checked the original material he informed me that the following corrections should be made to bring the nomenclature up to date, and to rectify some misidentifications:

p. 44 line 11 from below: *Nymphon grossipis* F, should read *N. rubrum* Hodge 1862.
Pycnogonum femoratum (Rathke), should read *Phoxichilidium femoratum* (Rathke 1799).

p. 121 *Pallene brevirostris* Johnston, should read *Callipallene brevirostris brevirostris* (Johnston 1837).

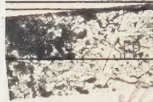
Anoplodactylus petiolatus (Hodge), should read *A. pygmaeus* (Hodge 1864).

Nymphon brevirostre Hodge, should read *N. rubrum* Hodge 1862.

Tables: *Anoplodactylus petiolatus*, should read *A. pygmaeus*.

P. KORRINGA

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